



Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England

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Synopsis

The palaeontology, sedimentology and stratigraphy of the Insect Bed (Bembridge Marls) are discussed and previous work summarized. Five insect orders are revised, notes on the biology of living relatives are included and the palaeoecology considered. Isoptera: *Mastotermes anglicus* von Rosen is redescribed, *Sisyra* (?) *disrupta* Cockerell is transferred from the Neuroptera to *Kaloterms* s. lat. (Kalotermitidae); a species of *Reticulitermes* (Rhinotermitidae) and a termitid are described but not named. The Isoptera suggest a warm subtropical-tropical climate. Plecoptera: *Nemoura priscula* Cockerell is transferred to the genus *Leuctra* (Leuctridae). Megaloptera: the record of *Raphidia* is shown to be erroneous. Neuroptera: Mantispidae: *Mantispa relicta* Cockerell is transferred to *Promantispa* gen. nov. Hemerobiidae: *Hemerobius tinctus* sp. nov., ? *Neuronema* spp. A and B, and 3 unnamed species are described. Chrysopidae: a species of Chrysopinae (s. lat.) is described but not named. The affinities of an extinct sisyrid are discussed. Mecoptera: *Panorpa veterna* Cockerell (Panorpidae) is transferred to the genus *Bittacus* (Bittacidae); an unnamed species of *Bittacus* is described. Lepidoptera: *Micropterix anglica* sp. nov.

(Micropterigidae), *Paratriaxomasia solentensis* gen. et sp. nov. (Tineidae), *Copromorpha fossilis* sp. nov. (Copromorphidae), *Pyralites preecei* sp. nov. (Pyralidae), *Nymphalites zeuneri* sp. nov. (Nymphalidae), *Prohepialus* sp. (Hepialidae) and *Geometridites larentiformis* sp. nov. (Geometridae) are described. *Lithopsyche antiqua* Butler is transferred to the Lycaenidae and the placement of *Gurnetia durranti* Cockerell in the Cossidae is questioned. A tineid, a tentative gelechioid, 12 other species of microlepidoptera and a possible papilionoid are described but not named.

Introduction

The Bembridge Marls are a predominantly argillaceous formation, 21–36 m thick, preserved only in the northerly half of the Isle of Wight in southern England (Fig. 1). Near the base of the formation is a thin clay bed, generally less than a metre thick, with concretions and tabular bands of fine-grained argillaceous limestone and hard marl. The latter, on the NW coast near Cowes, have been noted for their insect remains for just over a century and constitute the 'Insect Limestone' of authors (Daley 1973a). However, the calcareous and argillaceous developments together

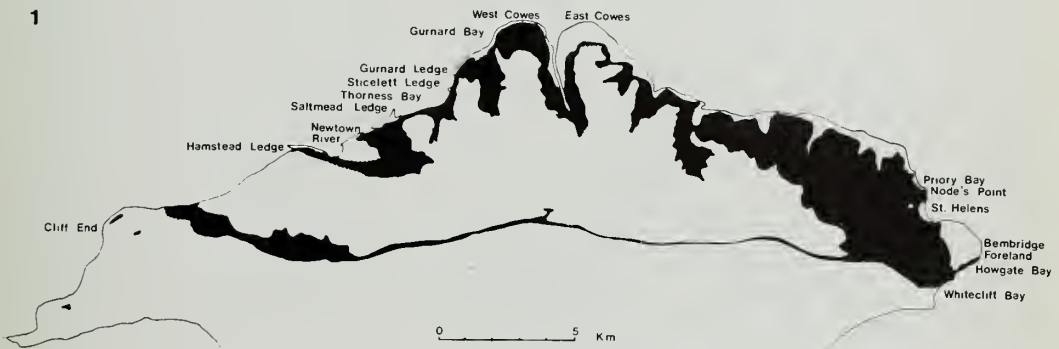


Fig. 1 Outcrop map of the Bembridge Marls.

form a distinct unit (*ibid.*) and the name Insect Bed (Bembridge Marls) used by Curry (1958) for a single limestone is here applied collectively. This horizon has yielded the only sizeable insect fauna in the British Tertiaries above the Lower Eocene, some fifteen orders being represented. The fauna also includes molluscs, an ostracod, an anostracous crustacean, an isopod, arachnids (spiders) and avian remains (feathers, Fig. 61, p. 268), the last three of which are scarce. Although named after the insects, the bed is probably better known in the palaeontological literature for its flora due to the work of Reid & Chandler (1926). However, apart from the leaves of a reed, well-preserved plant macrofossils are rare. Insect fragments are fairly frequent, and richer pockets are sometimes encountered (Jarzembowski 1976). The most extensive collections from this bed are now preserved in the British Museum (Natural History). These were largely collected by E. J. A'Court Smith (1814–1900), collecting between West Cowes and the Newtown River from about 1859 (Smith 1874). Apparently he discovered the insects following a comment by Forbes (1856 : 58–59) on the insect-bearing nature of some similar limestones in the Purbeck Beds (late Jurassic–early Cretaceous) on the mainland (Hughes 1922 : 67; Jackson 1933). Much of A'Court Smith's material subsequently went to R. W. Hooley and the Rev. P. B. Brodie, and the history of the collections and their acquisition by the Museum are given in Reid & Chandler (1926) and Crane & Getty (1975). Notable smaller collections from the Insect Bed include one at the Museum of Isle of Wight Geology, which was mainly the work of G. W. Colenutt, and another consisting of some of Brodie's material in the Lacoe Collection at the United States National Museum; I have myself collected from the bed since 1966.

The fossil insect collections at the British Museum (Natural History) contain over 3900 pieces of 'Insect Limestone' of which a large proportion bear two or more specimens. However, a

number of these are indeterminate and some species, especially in the Formicidae, are represented by numerous examples. The present paper is confined to the Isoptera, Plecoptera, Neuroptera, Mecoptera and Lepidoptera, which although rare or uncommon have yielded a varied range of taxa; several other orders are being studied. All available material is documented, and in addition to systematic and taxonomic considerations, the ecological and biological requirements of Recent relatives are briefly discussed.

Previous studies

A'Court Smith (1874) appears to be the first published record of the occurrence of arthropod remains in the Insect Bed near Cowes. Woodward (1878, 1879) published a list of identifications made by Frederick Smith of the Department of Zoology, British Museum (Natural History), based on a sample of A'Court Smith's collection. In the 1879 paper Woodward described an anostracan, *Branchipodites vectensis*, and an isopod, *Eosphaeroma fluviatile*, from the same horizon; Martini (1972) showed the latter to be a synonym of the continental species *Eosphaeroma margarum* (Desmarest 1822). McCook (1888*a, b*) gave two identical descriptions of a mygalomorph spider, *Eoatypus woodwardii*, and Jones & Sherborn (1889) described an ostracod *Potamocypris brodiei* which Haskins (1968) compared with *Cypridopsis*, another freshwater genus.

The first description of an insect, *Lithopsyche antiqua* Butler 1889, was accompanied by a colour plate. This was followed by von Rosen (1913) on fossil *Mastoterme*s, and in 1915, T. D. A. Cockerell described 33 new insect species from the Lacoë Collection. He subsequently made selective studies of the main collection at the BM(NH): Cockerell (1917*a*, 1921*a, b, c*, 1922); Cockerell & Andrews (1916); Cockerell & Haines (1921). The Formicidae were studied by Donisthorpe (1920), the Culicidae by Edwards (1923) and Orthoptera by Zeuner (1939). These constitute the main works on the insect fauna and, although the flora was monographed by Reid & Chandler (1926), there is no comprehensive work on the arthropods. Chandler (1964) reviewed the Bembridge Flora, including the microfloral work of Machin (née Pallot) published later in 1971. Although the junction of the Bembridge Marls and Bembridge Limestone is unconformable (Daley & Edwards 1971), the palaeobotanists considered the Bembridge Beds to contain a single flora, and it is not always clear which taxa occur in the Insect Bed. Daley (1969) studied the palaeoenvironment of the Bembridge Marls, and (1971, 1972*a*) was specifically concerned with sedimentary deformational structures in the 'Insect Limestone'. Jarzembowski (1976) first recorded insects in this bed on the east side of the island near St Helens, 18 km from Cowes.

Notes on lithology, inclusions and method of study

The insect-bearing lithology is usually a fine-grained argillaceous limestone with a conchoidal fracture and blue-grey colouration when fresh. It weathers externally producing a distinctive brownish yellow rind, and on broken surfaces the weathered zone has a sharp junction with the unweathered material. Older pebbles, especially near West Cowes, may only have a small region of 'blue' near the centre, and the weathered zone occasionally shows concentric colour banding. At outcrop it occurs in dark blue-grey clay as oval concretions, up to 20 cm thick, or as thinner tabular bands, and can be of a more marly constitution; thin, laterally continuous shell bands delimit the bed (Figs 2-4, p. 242). The calcareous developments tend to occur in courses within the clay more or less parallel to the bedding, which is of local stratigraphic value. There is a definite arching of the upper shell bed over large concretions, but in some places the undulations are less easy to explain.

Silty laminae, 1-4 mm thick and 3-90 mm apart, are usually evident in the limestone, marked by finely-comminuted carbonaceous detritus. They appear to have no vertical regularity and erosional bases are occasionally evident. The laminae may contain ostracod valves, fragments of drifted vegetation - the only common recognizable ones being of *Typha latissima* Braun - and insect wings and body fragments; groups of shells belonging to the freshwater genus *Galba* some-

times occur. The freshwater genera *Hippeutis* and *Viviparus* also occur but are infrequent. Plant fossils are usually accompanied by a brown carbonaceous residue, and small black fragments of vegetable material are occasionally present. One of the latter has been examined and identified as natural fusain by Professor T. M. Harris. The limestone has yielded some small grains of resin: one of these (In. 17436) was analysed by infrared spectroscopy, but the spectra obtained were too weak for comparison with those of other Tertiary resins.

The laminae occasionally yield concentrates of articulated insect bodies, often associated with abundant, complete examples of *Branchipodites vectensis*, but such rich developments appear to be very local. Salt pseudomorphs, comminuted shell debris, seeds, spiders and portions of bird feathers are rare: the last are the only vertebrate fossils found. Insect bodies and wings are normally preserved in good relief, although substantial compression is evident in some of the more argillaceous laminae; well-preserved insects as well as fragments occur in the interbedded limestone, but there is never any concentration of material. Chitin is absent only from weakly sclerotized areas and the colour pattern may be well preserved: comparison with related forms in the living fauna indicates that some colours are close to those in life (pp. 259, 262). The body cavities are often infilled with a pink calcareous material which obscures structures, but external moulds in the enclosing matrix show very fine detail (Fig. 59, p. 267) and the 'Insect Limestone' has been justifiably referred to as 'opaque amber'.

The insects are predominantly imagines of small to medium size. The preservation of relief and soft-bodied, immature stages (Fig. 62, p. 268) as well as the fragile *Branchipus*-like crustacean, together with the arching of the upper shell bed, indicate early lithification of the matrix, but the occasional penetration of burrows from above, and development of the small-scale sedimentary deformation described by Daley (1971, 1972a) and evident in the limestone at all the main localities, suggest that it was not immediate. Pantin (1958) provides evidence for the length of time involved in the formation of diagenetic calcareous concretions. It is likely that the limestone was formed within several thousand years of deposition of the sediment, and perhaps less judged by the preservation of the soft-bodied arthropods. I have not observed any insect macrofossils in the clays adjacent to fossiliferous concretions although a similar lamination is evident on fresh surfaces.

The remarks so far are based on the north-western localities. Whilst the lithological comments apply equally well on the east coast, there are some differences in the biota. St Helens and Priory Bay have yielded five orders of insects but only a few more complete specimens and the occasional ostracod and plant fragment. The author has only collected here since late 1975 and it is likely that more will be found. However, sustained search near Bembridge Foreland has yielded only a single insect specimen (see p. 243). Whilst the calcareous part of the Insect Bed is well developed and can be traced south into Whitecliff Bay, no fossils were found except for two fragments of lymnaean shell near the middle of Howgate Bay. The fossiliferous localities for insects are therefore confined to the northern part of the outcrop area of the Bembridge Marls (Fig. 1). Insect remains do occur at other levels in the formation, but very few specimens have been found to date. The A'Court Smith collection includes examples in a clay-ironstone matrix from the north-west coast, and I have seen one or two fragments in the sideritic ironstone concretions from the upper part of the Bembridge Marls littering the shore near Whitecliff Bay Point (Daley 1973b).

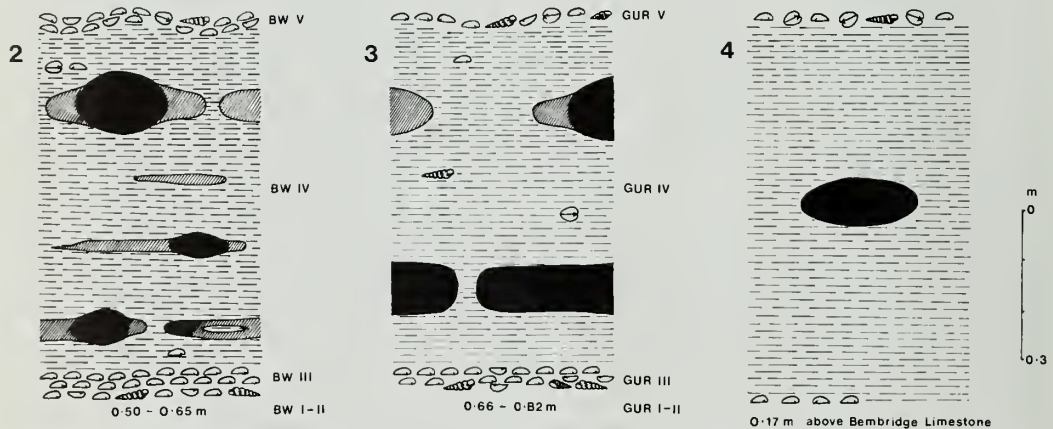
Where the limestone is exposed in the lower part of a cliff or slump and is accessible to marine erosion, it is usually well represented amongst the blocks and pebbles of the upper part of the shore, and splitting of this debris can be more rewarding. A hand-lens is necessary for examining fractured surfaces and small forms are more readily observed in oblique light. Specimens are rarely exposed properly owing to the curved fracture of the rock and both halves may show unique features. All the necessary preparation for this study was done by the author under a microscope with an electric engraver (vibrotol) or a tungsten needle. Routine examination of rock specimens under the microscope ($\times 16$) also revealed a number of forms previously unnoticed. The examination of chitinous material was often facilitated by immersing the specimen in liquid to heighten contrast; as the matrix may contain salt, especially the softer limestone and

hard marl, aqueous solutions were avoided and xylene was used for short examinations and paraffin for longer periods. Dry examination was also aided by using oblique lighting from several directions and referring to modern specimens of related forms.

Field sections

Natural exposures of the Insect Bed are confined to coastal sections and there appear to be no inland records from artificial excavations. The sections were examined between summer 1976 and spring 1977.

North-west coast. The 'Insect Limestone' is developed here only to the east of the Newtown River (Fig. 1, p. 239). The Insect Bed is represented by a thin band of clay just west of the river behind Hamstead Ledge and appears to be absent at Cliff End (Daley 1973a). Across the river, the strata descend gently on the eastern limb of the Porchfield anticline and the bed is seen at 433927¹, a short distance before the western end of Saltmead Ledge. It is exposed in the lower part of the cliff for some 500 m as far east as 438928 and fossiliferous blocks occur on the shore. The bed is 0.65–0.85 m thick and four calcareous courses are recognizable (Fig. 2). The uppermost includes some large concretions and may account for the thinness of the course below. At 440930 two blocks of limestone were seen apparently *in situ* in the upper part of the foreshore. Pebbles of 'Insect Limestone' die out on the beach a short distance east of Saltmead Ledge (=Thorness Point/Ledge).



Figs 2–4 Sections of the basal part of the Bembridge Marls. Fig. 2, near Saltmead Ledge. Fig. 3, immediately south of Gurnard Ledge. Fig. 4, near St Helens. (Black: limestone. Oblique shading: hard marl. Dashed lines: laminated marly clay. Bivalve: Corbiculidae. Small gastropod: *Tarebia*. Large gastropod: *Potamides*. The bed numbers to the right of Figs 2–3 are after Daley 1973a).

The bed is next seen on the east side of Thorness (=Thorney) Bay, where a limestone course outcrops on the upper part of the foreshore behind Sticelett Ledge (461941). The bed gradually rises from the shore north towards Gurnard Ledge (= Gurnard Point) on the northern limb of the Thorness syncline and is about 2 m above cliff base behind the latter (463946). It is best exposed in the low cliff for some 140 m south of the ledge and is 0.65–0.75 m thick. Two calcareous courses are developed: a lower more or less continuous tabular band of limestone (Insect Bed of Curry 1958) and an upper discontinuous band of concretions, often less well cemented (Fig. 3). The clay yields sporadic examples of worn *Potamides* and corbiculid valves, rare examples of the latter also being found in the calcareous part. Between Gurnard Ledge and Gurnard (=Gurnet) Bay there is a kilometre of tumbled cliff line in the Bembridge Beds but there are no further

¹ National Grid Reference, 100 km square 40 (SZ), as are the subsequent references.

sections in the Insect Bed on the northern coast of the island before St Helens. Some characteristic limestone was however found at several points amongst the slips 500–800 m NE of Gurnard Ledge, rising towards Gurnard from approximately 6 to 11 m above cliff base. Pieces of fossiliferous limestone occur amongst the shore débris as far as West Cowes (490966).

A Court Smith worked along the coast from West Cowes to the Newtown River (White 1921) although the specimens are generally labelled 'Gurnet (or Gurnard) Bay'. The most important collecting site was on the east side of Thorness Bay where the limestone outcropped on the shore (Brodie 1878, Reid 1889), which suggests that it was at Sticelett Ledge, and the latter has recently produced some relatively well-preserved material (Jarzembowski 1976). G. W. Colenutt refers to the site as Sticelett in correspondence (*ibid.*) but an accompanying sketch map by the same author is less helpful.

East Coast. Commencing in the north, a section of the Insect Bed is found NE of St Helen's Church (Fig. 4), 200–300 m south of Node's Point (638900). Although numerous blocks of limestone occur in the SW corner of the adjacent Priory Bay, no sections were observed amongst the slips. At the Point the bed is 9 m above the base of the cliff, and 0.7 m at the southern end of the section as the strata dip towards the axis of the Bembridge syncline. It is 0.60–0.85 m thick with a single course of limestone concretions. The lower shell bed is only well-developed in the southern part of the section.

Continuing south, the Insect Bed is next seen near Bembridge Foreland, 2.7 km SE of St Helens, where a limestone course outcrops on the upper part of the foreshore amongst the beach cover and can be traced into Howgate Bay. At 654872 the limestone is 15 cm thick and yielded a single *Oecophylla* wing. Further south the bed is seen in the lower part of the cliff near Whitecliff Bay Point, gradually ascending to the cliff top in Whitecliff Bay: the limestone becomes replaced by a more marly course, and there are no insect remains.

Correlation

Edwards (1966) gives a summary of the stratigraphy of the younger Palaeogene strata of the Hampshire Basin and an extensive bibliography is found in Edwards (1971). The Bembridge Marls are near to the Eocene–Oligocene boundary, but different workers have drawn it variously above and below the formation. Edwards (1966) followed Curry (1958) who regarded the Bembridge Marls as of Oligocene, Lattorfian age, but as can be seen from Table 1, there is still no general agreement on the position of the boundary. The Insect Bed (Bembridge Marls) can therefore be considered as of late Eocene or early Oligocene age, with an absolute dating of about 35 million years BP (cf. Cavalier & Pomerol 1977).

Table 1 The age of the Bembridge Marls according to various authors, 1966–76

| | |
|---|-------------------------------|
| Oligocene : Lattorfian | Edwards 1966 |
| Oligocene : Lattorfian | Curry 1966 |
| Middle Oligocene : early Rupelian | Rey 1967 |
| Lower Oligocene | Castel 1968 |
| Eocene : Ludian | Cavalier 1968 |
| Oligocene : Tongrian | Denizot 1968 |
| Upper Eocene or Lower Oligocene | Curry, Gulinck & Pomerol 1969 |
| Oligocene : Lattorfian | Daley 1969 |
| Oligocene : Tongrian | Haskins 1971 |
| Late Eocene–early Oligocene | Keen 1972 |
| Lower Oligocene | Martini 1972 |
| Late Eocene or early Oligocene | Bosma & Schmidt-Kittler 1972 |
| Late Eocene or early Oligocene | Bosma 1974 |
| Early Oligocene | Stinton 1975 |
| Upper Eocene : late Priabonian | Cavalier & Pomerol 1976 |

Systematic descriptions

The family and higher classification follows the papers of Gay, Riek and Common (all 1970) with the following departures: the Leucotrines are regarded as a family following modern usage, a superfamily classification of the Neuroptera is not adopted because of lack of general agreement, and the classification of the Lepidoptera is also based on Karsholt & Nielsen (1976).

Cockerell (1917*b* : 12) mentioned that he had described a species of *Raphidia* (order Megaloptera) from the Insect Bed; in fact (1917*a* : 373) he actually described a species of *Rhipidia* (order Diptera : Tipulidae) which is a mis-spelling of *Rhipidia* Meigen 1818.

A supplementary list of the material examined in the course of this study is deposited in the Palaeontology Library of the British Museum (Natural History). Except where otherwise indicated, the material is from the Insect Bed (Bembridge Marls) on the NW coast of the Isle of Wight, between West Cowes and the Newtown River. The figures prefixed 'I.' or 'In.' are registration numbers of the Department of Palaeontology, British Museum (Natural History) (BM(NH)) and the material is currently housed in the Department of Entomology at the same institution. The major collections are abbreviated thus:

S : E. J. A'Court Smith
 H : R. W. Hooley
 B : P. B. Brodie
 MIWG : Museum of Isle of Wight Geology

Other collections are named in full.

Wing veins are referred to by standard abbreviations; damaged or faint veins or margins are indicated by dashed lines, folds by dashed-and-dotted lines and extrapolations by dotted lines.

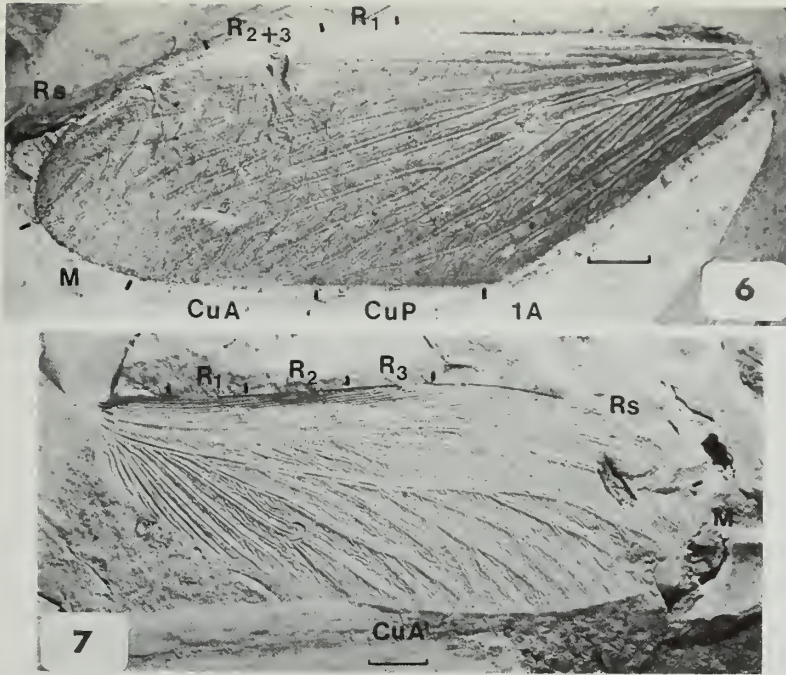
Order ISOPTERA Family MASTOTERMITIDAE

Genus *MASTOTERMES* Froggatt, 1896

TYPE SPECIES. *Mastotermes darwiniensis* Froggatt 1896 by monotypy; Recent, Australia.



Fig. 5 *Mastotermes anglicus* von Rosen. In.24571. (Scale line = 2 mm)



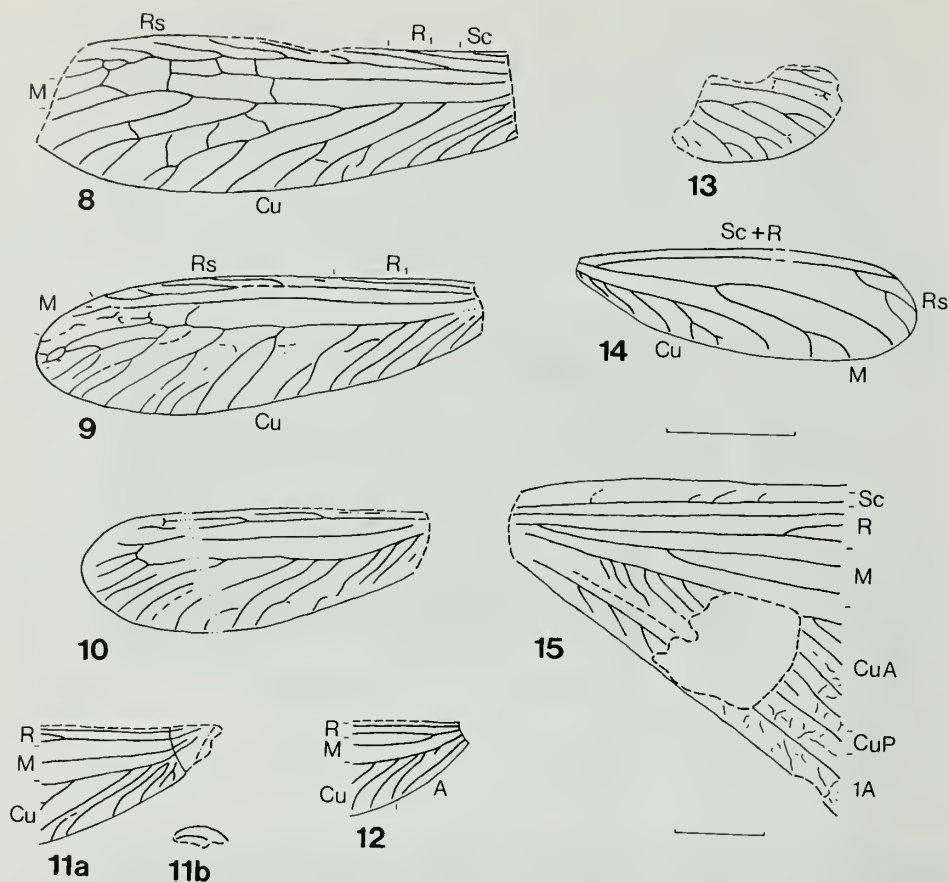
Figs 6-7 *Mastotermes anglicus* von Rosen. Fig. 6, lectotype (hindwing), I.15037. Fig. 7, paralectotype (forewing), I.15033. (Scale line = 2 mm)

Mastotermes anglicus von Rosen
Figs 5-7, 15, 20

- 1879 *Phryganea* F. Smith in Woodward : 344.
1913 *Mastotermes anglicus* von Rosen : 322; pl. 27, figs 5-8.
1965 = *Mastotermes batheri* von Rosen 1913; Emerson : 29.

EMENDED DESCRIPTION. *Forewing*: elongate, some incomplete specimens suggesting that a greater elongation is possible than in the specimen figured by von Rosen (1913 : pl. 27, fig. 7). Sc short and single. R_1 forking distad or basad of humeral suture, the outer branch terminating on the anterior margin at 0.2-0.4 of the forewing length (as measured from the suture). R_2 and R_3 elongate and separate at suture, R_2 sometimes forked. Stem of R_s terminating near wing apex with a more or less marked anterior curve in its distal part. R_s with about four branches to the anterior margin, the outer ones usually subdivided. M and Cu separate at suture, the former closer to R_s than CuA with one to three major branches distally and perhaps several short branches towards base. In the left forewing of In.17143 and right forewing of I.8659, M is briefly linked with R_s near base. R_s and CuA are closer in some specimens than in von Rosen's figure with M nearly median. CuA occupies about half of the wing area, dividing some ten times, the branches frequently forking once and occasionally several times. Humeral suture arcuate with maximum apical extension near M, and the basal part of the forewing is usually downcurved anterior to R_s . A brown pigmentation is often preserved on the scale, parts of M and on the more anterior veins. Forewings are preserved in 24 specimens and probably in two others.

Hindwing: elongate, rounded apically; anterior and posterior margins nearly parallel, apex nearer the latter. Sc single, elongate, on average about five times as long as in the forewing; some faint branches to the anterior margin may be present. R_1 long terminating at 0.6 of the wing length from base, with none to four subparallel branches. R_{2+3} has a common stem with R_s and



Figs 8–13 *Kalotermes disruptus* (Cockerell) comb. nov. Fig. 8, In.64534 (forewing). See also Fig. 17. Fig. 9, In.24619 (? hindwing). Fig. 10, In.24591 + In.24600 (hindwing). Fig. 11a, 1.9845 (right forewing base). Fig. 11b, 1.9845 (left forewing, anterior part of scale). Fig. 12, 1.9576 (hindwing base). Fig. 13, 1.8644 (holotype). See also Fig. 19.

Fig. 14 *Termitidae* species A, In.24603. See also Fig. 35.

Fig. 15 *Mastotermes anglicus* von Rosen, In.24610 (hindwing base).

(Scale line = 2 mm. Figs 8–14 same scale, minor reticulation and membranous irregularities omitted).

the appearance of being the first branch of the latter. Stem of Rs more or less oblique towards apex with two to four unforked major branches to the anterior margin. Stem of M nearer Rs than CuA, united with Rs at base, and producing two to three major branches to the apical part of the posterior margin. Some very short branches are developed towards the base of M. CuA dividing ten to eleven times, the branches becoming progressively shorter towards base. CuP single with a broad terminal fork. 1A parallel to anal fold with numerous short branches directed obliquely towards the latter. Anal lobe unknown, probably because it is folded under or broken away. The stem of M and the more anterior veins may show traces of brown pigmentation. As in the forewing, there is a well-developed reticulation. In addition to the lectotype, the hindwings are seen in six specimens and probably in two others.

Body: about 15 mm long and all parts pigmented brown as in Recent *Mastotermes*. Head with a well-defined Y-shaped suture. Antennae about 5.0 mm long, segments transversely oval near base, circular near middle and elongate distally. Pronotum widest anteriorly with sides strongly

downcurved (Fig. 20, p. 249). In 17357 has a longitudinal groove on the underside of the abdomen near the lateral margins as in Recent *Mastotermes*. In the same specimen, sternite 7 is not enlarged, indicating that it is a male. Body remains are preserved in 17 specimens.

LECTOTYPE. I.15037 (S), designated herein. Fig. 6.

OTHER MATERIAL. There are 18 paralectotypes and 42 other specimens (including one from St Helens), plus three possible specimens.

DIMENSIONS. Lectotype: wing length (apex—approximate position of 'suture') 25.8 mm, width 8.8 mm.

Other material. *Forewing*: length from humeral suture to apex (single specimen) 20.8 mm, maximum width 7.8–8.8 mm, length of Sc 1.0–2.8 mm, maximum length of scale 2.8–3.2 mm. *Hindwing*: length from wing base to apex 27.2–29.1 mm, maximum width 8.5–8.8 mm. *Body*: head, length 3.2–4.0 mm, maximum width 2.8–3.2 mm; pronotum, length 1.9–2.0 mm, maximum width 2.8–3.8 mm.

REMARKS. Emerson (1965 : 30) states that he examined the 'holotype' and 'paratypes' of *M. anglicus* and that the species was described from three specimens. Examination of the fossil insect collection at the BM(NH) showed that three specimens of this species, labelled 'holotype' (I.15037) and 'paratype' (I.15033 and I.8989), had been singled out and in addition there were a further 18 specimens each labelled 'paratype'. Von Rosen (1913 : 321) stated that he had examined 21 specimens of *M. anglicus*, and the former three correspond to the figures of his pl. 27; a footnote (1913 : 335) says that these are 'nach den Typen', but no holotype is designated in the paper. In a reprint from von Rosen in the library of the Department of Palaeontology, BM(NH), the registration numbers of the 21 specimens are hand written in the margin; I.15037 is indicated as 'type' and the remainder as 'paratypes'. Von Rosen's material is therefore a syntypic series and I.15037 is here designated as lectotype. However, only 18 paralectotypes are recognized, as there are two pairs of part and counterpart; a further 42 specimens from the Insect Bed are also referred to this species. Eight specimens from the A'Court Smith collection, purchased in 1883 (I.15034–6, I.15038–42) are labelled 'Phryganea', with or without a roman numeral in the same unidentified hand. Woodward (1879) recorded eight specimens of the trichopterous genus *Phryganea* in the A'Court Smith collection, on the basis of which a predator and prey association with *Branchipodites vectensis* was inferred by Tasch (1969). This misidentification was, however, realized not long afterwards, for on I.8804 Brodie had written 'Phryganea' which he then crossed out and replaced by 'termite'; the specimen was purchased in 1898, a year after his death. The lectotype, a single hindwing, is adequately figured by von Rosen (1913 : pl. 27, fig. 8) except that Sc probably continues apically for twice the figured length but is intertwined with the fine anterior branches from R₁.

Both the wing and body remains indicate that *M. anglicus* is close to the living *M. darwiniensis*. The wing venation of modern primitive termites is prone to individual variation and this was also true of *anglicus*. Emerson (1965) was probably aware of the difficulty of separating the two species when he stated '*Mastotermes anglicus* seems to have a greater proportional distance between the costal border and the radial sector than does *M. darwiniensis*' (1965 : 30). The distance from the stem of R_s to the anterior margin divided by the wing width, measured near the mid-point of the wing, gave values of 0.14–0.18 and 0.15–0.18 for the fore- and hindwings respectively of the fossil species. This compares very well with the living species (cf. Gay 1970 : fig. 15.2; von Rosen 1913 : pl. 26, figs 1–2; Tillyard 1931 : pl. 21, figs 1–2). *M. anglicus* appears to differ from *M. darwiniensis* in that more branches of CuA originate directly from the main stem in the forewing: in the latter there are five–six main branches. The soldier caste is generally more useful for separating species in modern termites but only the reproductives are so far known from the Isle of Wight.

Present day *Mastotermes* is naturally confined to tropical northern Australia, although it has been introduced to New Guinea, its southern limit being the Tropic of Capricorn. The termite avoids high-rainfall areas and is absent from rainforest and areas where such forest has been

cleared. It is very destructive of timber, although some trees including *Ficus* spp. are hardly affected; this genus is known from the Insect Bed (Reid & Chandler 1926; personal examination of matrix). The termite normally nests in or under the boles of trees, or in logs or stumps, and produces galleries in the soil. Alates are released in early November and have been recorded through the summer monsoon season (Gay & Calaby 1970 : 395-396).

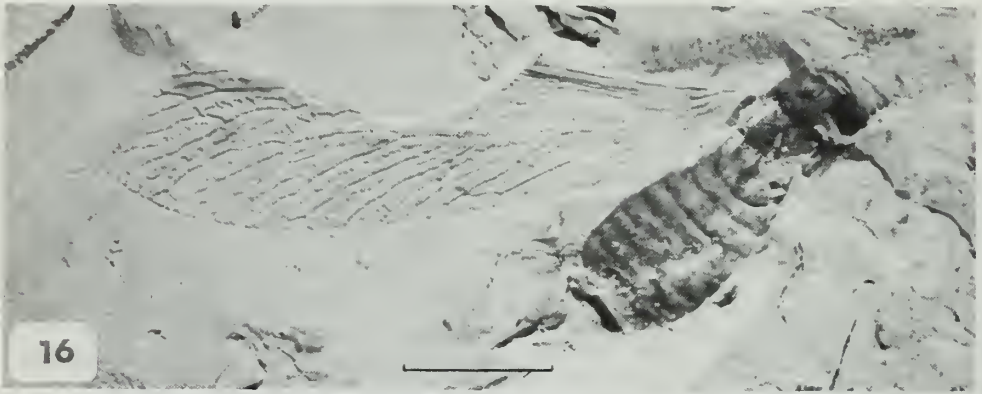


Fig. 16 *Kalotermea disruptus* (Cockerell) comb. nov. I.9845. (Scale line = 2 mm)

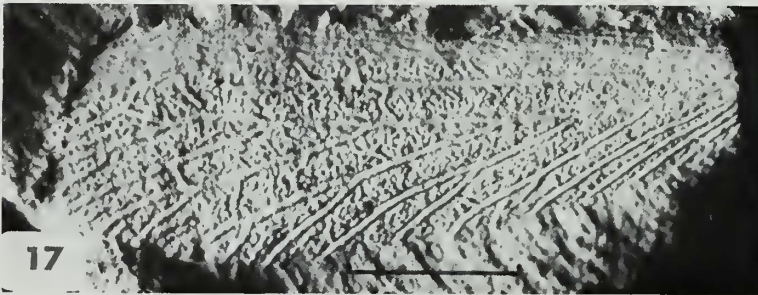


Fig. 17 *Kalotermea disruptus* (Cockerell) comb. nov. In.64534, forewing. See also Fig. 8. (Scale line = 2 mm)

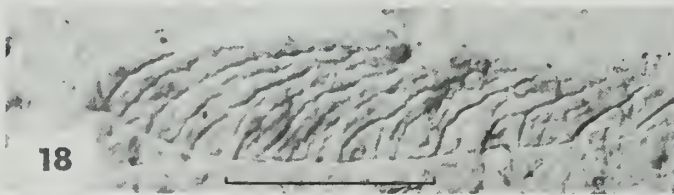


Fig. 18 In.64535, incomplete counterpart of a termite wing from the Insect Bed to show preservational similarity to Fig. 19.

Fig. 19 *Kalotermea disruptus* (Cockerell) comb. nov. Holotype, posterior margin uppermost. See also Fig. 13. (Scale line = 2 mm)

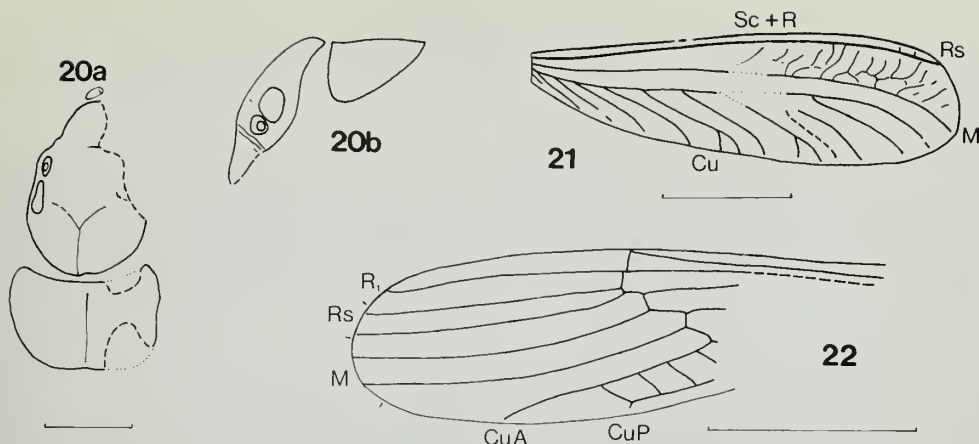


Fig. 20 *Mastotermes anglicus* von Rosen, In.43415, head and pronotum. Fig. 20a, dorsal view. Fig. 20b, lateral view.

Fig. 21 *Reticulitermes* sp., In.64535 (forewing). Venation and main reticulation only. See also Fig. 26.

Fig. 22 *Leuctra priscula* (Cockerell) comb. nov. Forewing venation. Holotype, In.17498. (Scale line = 2 mm)

Family KALOTERMITIDAE

Genus *KALOTERMES* Hagen, 1853

TYPE SPECIES. *Termes flavicolle* Fabricius 1793, by subsequent designation; Recent, western Palaearctic.

Kalotermes disruptus (Cockerell) comb. nov. Figs 8–13, 16–19

1917a *Sisyra* (?) *disrupta* Cockerell : 381; pl. 31, fig. 13.

EMENDED DESCRIPTION. The holotype consists of an apical fragment of a wing with parts of Cu, M and possibly Rs preserved. The following account is based on a series of specimens considered to be conspecific with the type.

The body is known from a single dorsal impression (I.9845). The head is missing except for traces of the basal region which indicate that it was inclined downwards at burial. Pronotum gently tapered anteriorly and with sides slightly curved ventrally; meso- and metanota subequal. Abdomen with nine visible segments, the ninth curved anteroposteriorly with blunt posterior angle. A single leg is preserved: tibia with remains of an inner terminal spur; tarsus with elongate distal segment and short basal segments.

Wings elongate, gradually widening towards the apex with maximum width at 0.3 of the length from the latter; apex rounded. R_1 single and close to the anterior margin. Costal area (stem of Rs to anterior margin) moderately wide and frequently downcurved especially near base as in Recent termites, and consequently difficult to examine. Rs with 3–6 oblique, single branches to the anterior margin. Cu occupies just over half of the wing area, branching 8–10 times. Branches of Cu running obliquely to the posterior margin and less inclined than those of Rs: they may fork once or occasionally twice at a variable distance from base. M nearly parallel to the stems of Rs and Cu, and slightly closer to the former. M may have a longish apical fork or two to three short terminal branches and may unite with Rs for a short distance apically. The terminations of Rs, M and Cu are often difficult to identify in the variable pattern of short veins or reticulations near the wing apex.

The wing membrane is finely tuberculate (in dorsal aspect) posterior to Rs; the sculpture may be well-defined (Fig. 17), or only a general irregularity of the surface may be discernible. A few crossvein-like reticulations are also developed. R_1 , much of Rs and the basal portions of M and Cu often show traces of a dark brown pigmentation apparently corresponding to the more sclerotized areas in life; body light brown.

Fore- and hindwings are not readily identifiable from incomplete specimens but the former are represented by I.9845 and In.64534, and the latter by I.9576, In.24591 + In.24600 and In.24621. The humeral suture in the forewing is gently curved towards base posterior to R_1 ; the forewing scale has a strongly curved anterior margin and overlaps the base of the hindwing scale (I.9845). The hindwing suture is shorter and more arcuate, Rs and M separate distad of the suture, A present.

HOLOTYPE. I.8644 (B). Figs 13, 19.

OTHER MATERIAL. 14 specimens and possibly one other.

DIMENSIONS. *Wings*: length (distance from humeral suture–apex) *c.* 6.0–8.1 mm, maximum width 2.0–2.4 mm.

Body (I.9845 only): length of thorax 2 mm, length of pronotum 0.7 mm, maximum width of pronotum 1.3 mm, maximum width of meso- and metathorax 1 mm; length of abdomen 2.6 mm; length of tibia 0.6 mm.

REMARKS. Cockerell described this species from a single wing fragment, and on the basis of a comparison with Recent *Sisyra vicaria* (Walker) it was placed in the Neuroptera (Hemerobiidae: Sisyriinae). He was, however, doubtful about its generic placement (Cockerell 1917a : 381–382).

Comparison of the fragment with *S. vicaria* and Recent *Sisyra* spp., and with fossil insects from the Insect Bed in the BM(NH), indicates that the species should be transferred to the Isoptera, because

- i. The vein pattern does not agree with Sisyridae (cf. Parfin & Gurney 1956);
- ii. Neither veins nor wing margin show any trace of macrotrichia or trichosors which are present in sisyrids (*ibid.*); preservational failure is improbable when compared with other Insect Bed Neuroptera;
- iii. The veins are relatively thick and lacking in pigmentation, unlike the Insect Bed Neuroptera;
- iv. *S. vicaria* and the Insect Bed Neuroptera may show a faint, linear fold in the membrane between two veins, but this is different from the membranous irregularities in Cockerell's specimen;
- v. The fragment compares best with the negative impressions of wings belonging to a hitherto unrecognized termite in which the venation is well developed near the apex.

The type and new material are referred to the family Kalotermitidae because the pronotum is flatly arched and not narrower than the head, the anterior wing scale overlaps the hindwing scale, Sc is short and sclerotized in the forewing and absent in the hindwing, R_1 is sclerotized and single, Rs is sclerotized and parallel to the anterior margin with a number of branches to the latter, Cu is unsclerotized with numerous branches to the posterior margin and an anal vein is present in the hindwing only (Krishna 1961 : 315).

The wing sculpture is similar to Recent *Glyptotermes* Froggatt, *Rugitermes* Holmgren and *Kalotermes*, and of these three, the venation comes closest to *Kalotermes* (Krishna 1961). However, the relatively small number of branches of Rs in the forewing (Fig. 8) is more like Recent *Incisitermes* Krishna than *Kalotermes* (Krishna 1961 : 334, 354). Krishna erected the former genus for a segregate of *Kalotermes* in which one of the diagnostic characters is the absence of tuberculation of the wing membrane. Emerson (1969 : 43, 49) accepted the new genus but rejected the distinction with regards to wing sculpture. Examination of the alates of *K. flavicollis* (Fabricius), *K. rufinotum* Hill, *I. minor* (Hagen) and *I. tabogae* (Snyder) suggests to me that sculpture does not always allow a definite separation of the two genera (Figs 23–24). In *Kalotermes rhenanus* Hagen from the Oligocene of Rott, Germany, Rs has 5–8 branches in the forewing and 3–4 in the hindwing

(Emerson 1969 : 34), which compares well with the Bembridge Marls species (Figs 8–10). However, there appears to be no indication of wing sculpture in *K. rhenanus*. The costal area of the forewing is too poorly known in *disruptus* for detailed comparison with the Recent genera. Emerson (1969 : 29) expresses some uncertainty about distinguishing alates of the two genera in fossils where the dentition is unknown, and the Bembridge Marls species is therefore referred to *Kaloterмес* in the wider sense.

The wings of kalotermitids are especially subject to variation (cf. Fuller 1919 : pl. 8, pl. 9 figs 124–134), and no two examples in *Kaloterмес disruptus* (Cockerell) comb. nov. are likely to be exactly similar in the finer details of venation and reticulation. Recent kalotermitids are xylophagous, predominantly dry-wood termites, digestion being made possible by an abundant intestinal fauna of flagellate Protozoa. *Incisiterмес* and *Kaloterмес* are both hardwood termites, the former occurring in the New World and across the western Pacific and the latter with a cosmopolitan distribution (Emerson 1969 : 45; fig. 11). *Incisiterмес* is warm temperate (sub-tropical)–tropical, but *Kaloterмес* is mainly temperate (*ibid* : 45, 49), although preferring the warmer part of that zone (*ibid* : fig. 7). The Kalotermitidae are represented in Europe at the present time by a single species restricted to southern parts (Harris 1970 : 297).

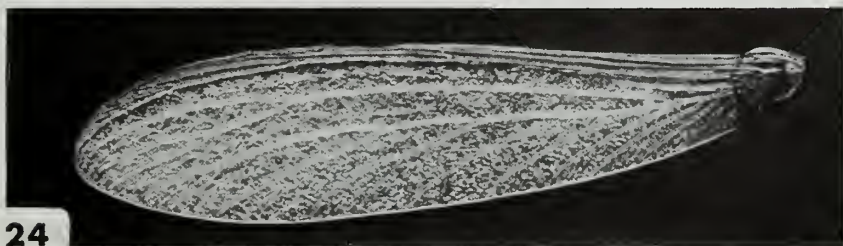
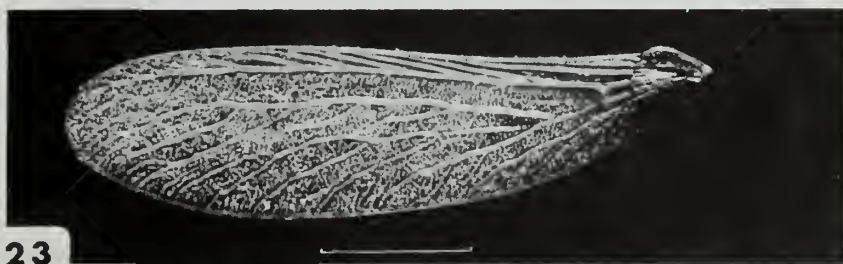


Fig. 23 *Kaloterмес flavicollis*. Recent; forewing. Oblique top lighting.

Fig. 24 *Incisiterмес tabogae*. Recent; forewing. Oblique top lighting, same scale as Fig. 23. (Scale line = 2 mm)

Family RHINOTERMITIDAE
Subfamily HETEROTERMITINAE

Genus *RETICULITERMES* Holmgren, 1913

TYPE SPECIES. *Termes flavipes* Kollar 1837 by subsequent designation; Recent, Holarctic.

Reticuliterмес sp.
Figs 21, 26

DESCRIPTION. The species is only known from wing material. Wings elongate, forewing with a length/width ratio of 4·3·3:1. Humeral suture nearly straight in forewing (In.17119, In.64535). Sc+R prominent forming the anterior margin. Rs prominent, close to Sc+R, terminating near

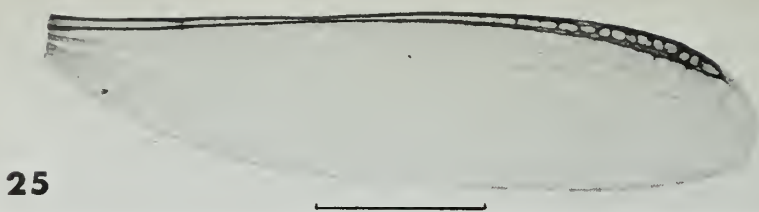


Fig. 25 *Reticulitermes tibialis*. Recent; forewing. Transmitted light. (Scale line = 2 mm)



Fig. 26 *Reticulitermes* sp., In.64535. See also Fig. 21. (Scale line = 2 mm)

the wing apex. Cu occupies nearly half the wing width, branching 8–10 times, some branches dividing again distally. M single, closer to Cu than Rs and parallel to the former, with a posterior curve apically.

Membrane reticulate posterior to Rs; a few incipient, transverse ridges may be discernible near the apical extremities of Rs and Sc + R. The reticulation is best developed in the distal part of the Rs space, consisting of oblique transverse ridges tending to join medially to form an irregular longitudinal ridge. Wing colouration : Sc + R and Rs brown along much of their length; Cu and M only pigmented near the suture.

In.24623 and In.25047 are relatively small wings and may represent a separate species.

In.24821 is probably a hindwing as Rs and M appear to meet just distad of the humeral suture and the wing is comparatively narrow near base, but the specimen is too poorly preserved to be referred to this species with certainty.

MATERIAL. Seven specimens and possibly one other.

DIMENSIONS. Forewing length 6.0–6.6 mm, width 1.5–2.0 mm. Length of humeral suture (forewing) 0.5 mm. (In.24623 length 4.5 mm, width 1.3 mm. In.25047 length 5 mm, width 1.4 mm).

REMARKS. The presence of reticulation, a comparatively reduced venation with Rs simple and parallel to the anterior margin, and general habitus place the wings in the Rhinotermitidae : Heterotermitinae. A well-defined, irregular transverse reticulation is like *Reticulitermes* Holmgren (Fig. 25) and unlike *Heterotermes* Froggatt (Banks & Snyder 1920 : 42; Hill 1942 : 121; Weesner 1970 : 495).

Recent *Reticulitermes* spp. are xylophagous insects tunnelling in pieces of damp wood which are frequently buried; adjacent pieces are linked by subterranean galleries (Noirot 1970 : 77). The Pysonymphidae, a family of intestinal Protozoa, are confined to *Reticulitermes*. The genus is mainly Holarctic, but there are a few oriental species (Roonwal 1970 : 334). It is essentially temperate; it normally occurs to latitude 46°N in Europe, a little further north than *Kalotermes* (Harris 1970 : 299) and occurs as far south as the borders of Vietnam where it inhabits mountainous regions (Harris 1968).

Species A
Figs 14, 35

DESCRIPTION. The material consists of a single wing broken off at the humeral suture. Wing narrow basally, apex rounded; humeral suture short, straight. Sc+R prominent, gently curved. Rs prominent, close and parallel to Sc+R for most of its course terminating just before the wing apex. Rs with a short, forked apical branch, but this is weak and not pigmented like the main stem. M separates from R a short distance beyond the suture; Cu relatively short, terminating near the mid-length of the wing and branching five times. Sc+R, Rs and base of Cu are brown-coloured. There is some faint reticulation of the wing membrane especially near the apex.

MATERIAL. In.24603 (H) (Figs 14, 35) and counterpart In.24596 (H).

DIMENSIONS. Maximum length 5.5 mm, width 1.6 mm. M divides 2.0 mm from base.

REMARKS. The simple venation, M well separated from Rs and close to Cu, and reduced reticulation are indicative of the higher termites (Termitidae). This is the largest family of Isoptera at the present day and is essentially tropical although some genera range into warm temperate regions (Harris 1970 : 309). Termitids are humivorous or phytophagous, the latter including wood feeders; nesting habits are varied (Noirot 1970).

The wing venation of the fossil approaches that of extant *Apicotermes occultus* Silvestri (Apicotermitinae); the reticulation suggests some affinity with the Macrotermitinae, e.g. *Microtermes* spp. The systematic position of the fossil within the family is uncertain and it may well represent an extinct genus.

Family Uncertain

In.24417 (H). Basal half of a wing, 9 mm long, with only the posterior part preserved, showing part of Cu and several branches. Membrane slightly tuberculate.

I.8648 (B), I.10204 (B), In.24414 (H), In.24612 (H) and counterpart In.25358 (H), In.24616 (H) and In.24618 (H) are indeterminate wing fragments belonging to the Kalotermitidae or Rhinotermitidae.

Order PLECOPTERA
Suborder FILIPALPIA
Family LEUCTRIDAE

Genus *LEUCTRA* Stephens, 1836

TYPE SPECIES. *Phryganea fusca* Linné 1758 by subsequent designation; Recent, Palearctic.

Leuctra priscula (Cockerell) comb. nov.
Fig. 22

1922 *Nemoura* (s. lat.) *priscula* Cockerell : 34; fig. 2.

EMENDED DESCRIPTION. Single specimen consisting of an incomplete forewing with the outer half and most of the anterior area preserved. Estimated original length 7 mm. Sc reaches anterior margin 2.75 mm from wing apex. Rs, M and Cu two-branched. Crossvein r-m originating just basad of the fork of Rs, m-cu from M_{3+4} just distad of the fork of M. Four Cu crossveins preserved, the only crossveins apical to the cord. Sc_2 and i.r nearly continuous and perpendicular to anterior margin.

HOLOTYPE. In.17498 (S). Fig. 22.

REMARKS. The venation is plecopteran of the *Leuctra* type (Needham & Claassen 1925 : pl. 2, fig. 21). It is distinguished from *Nemoura* Latreille by the absence of an oblique crossvein in the apical marginal space (*ibid.* : 196). The fossil is referred to *Leuctra* Stephens s. lat., the material

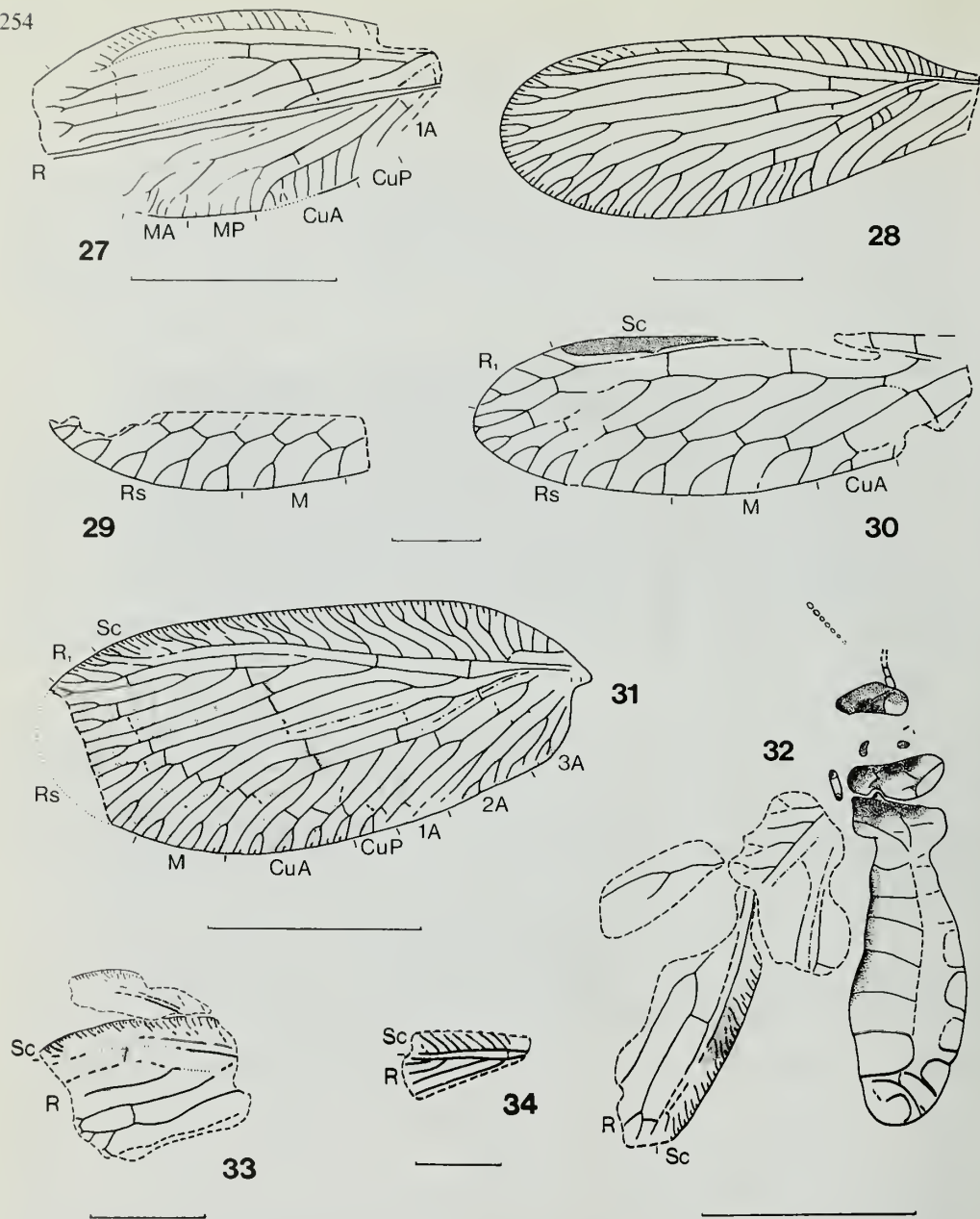


Fig. 27 *Sisyridae* species A, forewing. In.17287.

Fig. 28 *Sisyra fuscata* (Fabricius). Recent; forewing.

Figs 29-30 *Promantisa relict*a (Cockerell) gen. and comb. nov. Fig. 29, holotype, In.24326.

Fig. 30, In.24597 (forewing).

Fig. 31 *Hemerobius tinctus* n. sp. **Holotype**, I.9160.

Fig. 32 Hemerobiidae species B. The wings are in fact at a slight angle to the body but are drawn as if coplanar. In.17173.

Fig. 33 Hemerobiidae species A. In 43477.

Fig. 34 Hemerobiidae species C. In.17445.

(Scale line = 2 mm)

being too fragmentary for certain reference to any of the subgeneric or generic segregates of *Leuctra* currently recognized by entomologists.

Leuctrid adults are found amongst stones and foliage near freshwater streams, rivers and lakes which are the habitat of the aquatic nymphs. Both adults and young are herbivorous, the former feeding on lichens and small algae (Claassen 1931 : 97; Hynes 1941 : 529, 534, 547-548). The family is mainly Holarctic and the common name of needleflies stems from the adult habit of rolling the wings around the body in repose.

Order **NEUROPTERA**
Family **MANTISPIDAE**

Genus *PROMANTISPA* nov.

DIAGNOSIS. A Palaeogene genus of Mantispaenae differing from *Mantispa* Illiger in the possession of an apically extended pterostigma.

TYPE SPECIES. *Mantispa relictta* Cockerell 1921*b*.

Promantispa relictta (Cockerell) comb. nov.
Figs 29, 30

1921*b* *Mantispa relictta* Cockerell : 477-478; fig. 46.

EMENDED DESCRIPTION. The original description is based on a single wing fragment 7 mm long, preserving the distal portions of the branches of M and five branches of Rs, plus part of a gradate series of crossveins (Fig. 29). The veins are coloured brown and macrotrichial bases are visible on the veins and wing margin.

The discovery of an unrecognized left forewing (In.24597 + In.24631) requires a redescription of the species. During fossilization, the wing was broadly folded about a longitudinal axis and Fig. 30 is based on a combination of three *camera lucida* drawings from slightly different positions. Original length estimated at 15 mm. Costal area with basal expansion as usual in mantispid forewings, with two well-separated crossveins preserved. Sc curved posteriorly in its apical portion to form the posterior boundary of the pterostigma. The latter is pale brown, very elongate and blunt apically. Sc deflected towards R_1 just distad of 2nd r_1 - r_s indicating the position of a short pterostigmal crossvein at 0.4 of the length of the pterostigma from base. R_1 on prominent wing fold, close to Sc basally, and producing three oblique crossveins to the anterior margin beyond the pterostigma. Rs undulose, originating 10.0 mm from wing apex, with six branches to the outer posterolateral margin and three equidistant crossveins to R_1 partitioning the branches 1, 2, 2, 1. M dividing nearly opposite R with a short r - m crossvein a small distance distad of the fork; an oblique m - cu just basad of the fork is continuous with an incompletely preserved cubital crossvein. Branches of Rs, M and CuA_1 end-twigged and linked by one gradate series of crossveins; branches of Rs and MA undulose. CuA_2 short and apparently single.



Fig. 35 Termitidae species A, In.24603. See also Fig. 14. (Scale line = 2 mm)

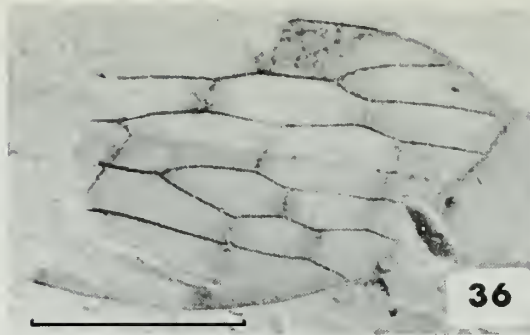


Fig. 36 *Bittacus veternus* (Cockerell) comb. nov. Holotype, In.24330, ventral half. See also Fig. 44. (Scale line = 2 mm)



Fig. 37 *Mantispa tenella* Erichson. Recent. (Scale line = 2 mm)



Fig. 38 *Prohepialus* sp., wing. In.17464. (Scale line = 2 mm)

Veins dark brown; macrotrichial bases visible on veins, pterostigma and wing margin; macrotrichial hairs preserved along the margin near the apex. Trichosors absent.

HOLOTYPE. In.24326 (H.15381). Fig. 29.

OTHER MATERIAL. In.24597 (Fig. 30) and incomplete counterpart In.24631 (H).

DIMENSIONS. Forewing: maximum length 11.5 mm, width 3.5 mm.

REMARKS. The *Mantispa*-like venation and absence of trichosors place the fossil in the Mantispidae : Mantispinae (Tjeder 1959 : 275). However, the pterostigma in *Mantispa* is relatively short (Handschin 1959 : 198) and usually has an obliquely truncate apical margin just beyond the pterostigmal crossvein. The pterostigma in the fossil bears some resemblance to *Ditaxis biseriata* (Westwood), but the venation of the latter is quite different. Comparison of the fossil with species representing all the known genera of Mantispidae (about 38) indicates that a new genus is required. *Promantispa relicta* (Cockerell) gen. and comb. nov. appears to be the only known fossil representative of the family.

Recent mantispids (mantis flies) are found in all major regions including Europe, but they no longer occur in Britain. The adults are found on vegetation where they are predacious on other insects, the raptorial forelegs (Fig. 37) having a striking convergence with those of mantids (praying mantises) and berotherids (Rachiberothinae). The older larvae of Mantispinae enter the egg sacs of spiders where they feed, hypermetamorphose and pupate (McKeown & Mincham 1948; Tjeder 1959 : 260, 273); the Order Araneida is represented in the Insect Bed.

Family HEMEROBIIDAE

Genus *HEMEROBIUS* Linné, 1758

TYPE SPECIES. *Hemerobius humulinus* Linné 1758, by subsequent designation; Recent, Holarctic.

Hemerobius tinctus sp. nov.

Fig. 31

DIAGNOSIS. A Palaeogene species of *Hemerobius* differing from *H. humulinus* in that the inner branch of Rs is divided near base and there is an sc-r crossvein near the base of the middle branch of Rs.

DESCRIPTION. The species is known from a single forewing and is smaller than *Hemerobius humulinus* (Killington 1936 : pl. 13) with an estimated forewing span of 11 mm. Costal area narrow, humeral vein recurved with four single branches to the anterior margin. Sc terminating on anterior margin and branching about 17 times. Rs arising from R on three branches, inner branch dividing close to base and outer branch separating near mid-point of wing; the latter branch with three main forks. Sc linked to stem of R by two crossveins immediately basad of the origins of the middle and inner branches of Rs. No basal r-m nor basal crossvein between the branches of Rs. MA and MP separating near the base of M, forking distally. CuA branching four times distally, CuP with a single fork. Two gradate series of crossveins present, outer series extending from R₁ to 1A. Veins with macrotrichia and usually end-twigged marginally. Trichosors present. Colour pattern consisting of a light brown pigmentation of the membrane especially in the outer part of the wing and tending to form transverse bands.

HOLOTYPE. I.9160 (B). Fig. 31.

DIMENSIONS. Forewing length 5.0 mm, maximum width 2.2 mm.

REMARKS. Rs arising on more than two stems, Sc terminating on the costal margin and general form of the wing place it in the family Hemerobiidae (Riek 1970). The fossil is close to the extant *Hemerobius humulinus* (Killington 1936 : fig. 11 ; pl. 13, fig. 3) but comparison with this and other *Hemerobius* spp. in the BM(NH) indicates that the basal fork of the inner branch of Rs and the

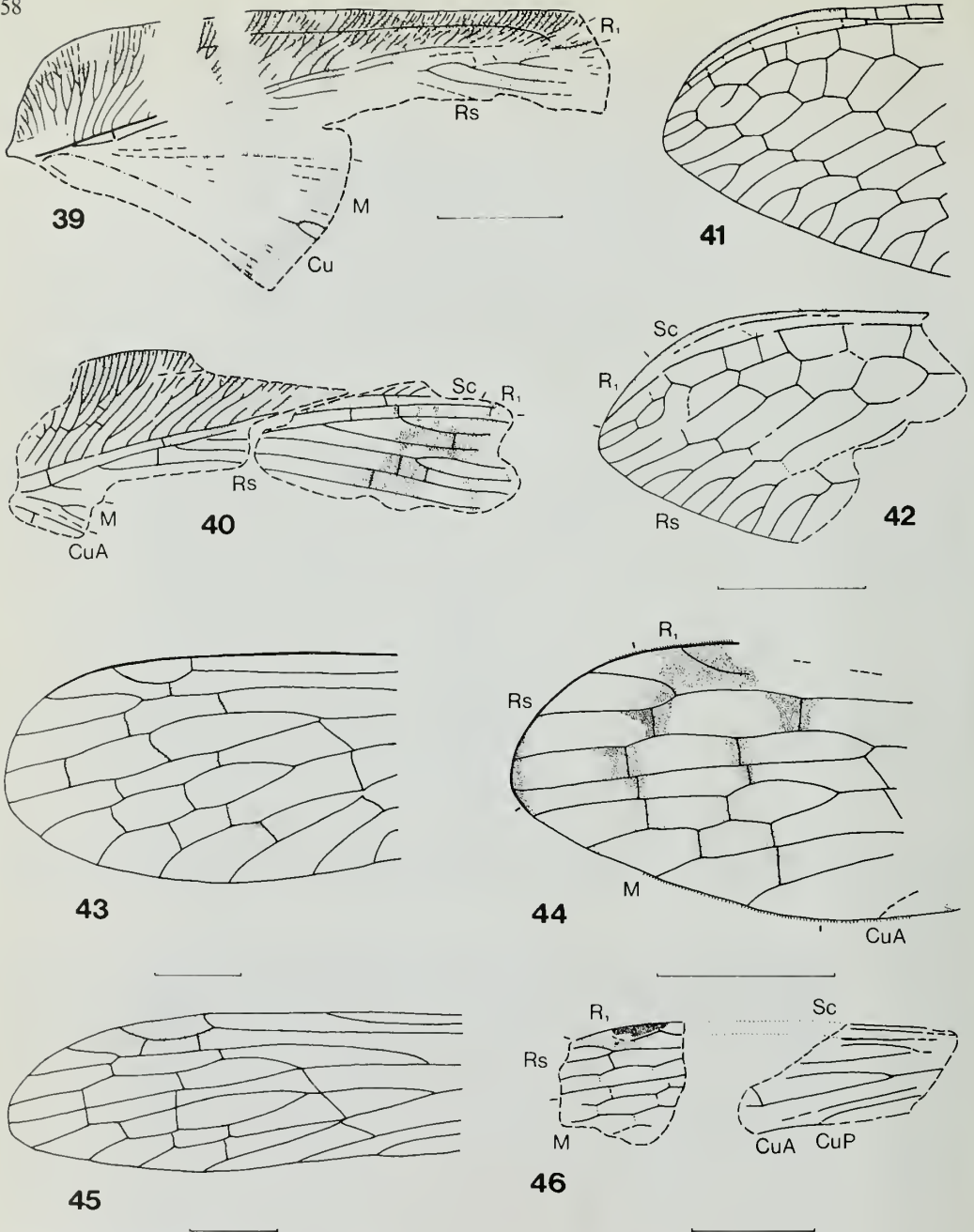


Fig. 39 ? *Neuronema* species A. In.17404.

Fig. 40 ? *Neuronema* species B. In.64536.

Fig. 41 *Nothochrysa capitata* (Fabricius). Recent; hindwing tip. The crossveins in the subcostal space are not prominent and less likely to be preserved if fossilized (cf. Fig. 42).

Fig. 42 Chrysopidae species A. I.8643.

Fig. 43 *Bittacus sinensis* Walker. Recent; forewing tip.

Fig. 44 *Bittacus veterenus* (Cockerell) comb. nov. Holotype, In.24330. See also Fig. 36.

Fig. 45 *Bittacus chlorostigma* McLachlan. Recent; outer part of forewing.

Fig. 46 *Bittacus* species A. In.64537.

(Scale line = 2 mm; Figs 39-41 are to same scale.)

crossvein near the base of the middle branch of R_s is unusual for the genus and may form the basis of a supraspecific grouping. The colouration of *H. tinctus* sp. nov. resembles Recent *H. atrifrons* McLachlan.

Recent hemerobiids (brown lacewings) are terrestrial insects and both adults and larvae prey on small soft-bodied arthropods. They are commonly arboreal but also occur on low herbage. The genus *Hemerobius* has a cosmopolitan distribution and can be economically important in the biological control of aphids (Balduf 1939 : 251–253, 256–257, 259; Tjeder 1961 : 296).

Genus *NEURONEMA* McLachlan, 1869

TYPE SPECIES. *Hemerobius decisus* Walker 1860, by original designation; Recent, Hindustan.

? *Neuronema* sp. A

Fig. 39

DESCRIPTION. The species is known from a single impression of an incomplete left forewing, original length estimated at about 12 mm. Costal area very broad near base, narrowing apically and with a distinctive longitudinal line as in some Recent hemerobiids. Costal crossveins numerous, usually forking once and often twice in their distal halves and becoming increasingly oblique towards apex. The first seven crossveins are evenly truncate at base, indicating the course of a strongly recurved humeral vein, although the vein itself is difficult to discern. Sc and stem of R are marked by strong folds in their proximal portions, flattening out distally and curving towards the apex. Subcostal area with a slight basal expansion. Five branches of R_s can be distinguished and the spacing indicates that this is close to the actual complement. Four to five branches of R_2 are discernible. The median area is bounded by a faint fold on its outer side and a prominent fold on its inner side. M and Cu indicated by some vague traces of venation. Colouration : dark brown mottles in costal area and traces of an oblique brown band across the wing; similar browns are typical in the wing colouration of Recent hemerobiids.

MATERIAL. In.17404 (S). Fig. 39.

DIMENSIONS. Forewing length 10.5 mm, maximum width 4.8 mm.

REMARKS. R_s arising on several branches from R is indicative of the Hemerobiidae (Fraser 1959 : 18; Riek 1970 : 482). The wide costal area, recurved humeral vein, R_s with four to six or seven branches, pectinate branching of R_2 and form of the costal crossveins place the fossil close to Recent *Drepanacra* and *Neuronema* (Nakahara 1960 : 61–62; pls 15–16), especially the latter oriental genus (e.g. *Neuronema irrorata* Kimmins).

Drepanacra Tillyard is an Australian genus and known to feed on *Neomyzaphis* Theobald (Balduf 1939).

? *Neuronema* sp. B

Fig. 40

DESCRIPTION. The fragmentary forewing is of a similar size and colouration to Species A. The costal area differs in that there are a few longitudinal crossveins towards base. A basal crossvein between Sc and R is present as well as two more apical crossveins. R_s arises on four branches, R_2 with three well-spaced forks. R_4 with basal crossvein to R stem, R_1 with three crossveins to R_2 stem. There are also several crossveins in the apical portions of R_2 – R_4 . M divides near base.

MATERIAL. In.64536 (E. A. Jarzembowski, J. Cooper and S. F. Morris). Fig. 40.

REMARKS. Species B is close to Species A but differs principally in the presence of the longitudinal crossveins in the costal area and R_2 appears to have fewer branches.

Genus *indet.*

Species A

Fig. 33

DESCRIPTION. The species is known from two fragments of the apico-anterior region of the wings. Forewing: three branches of Rs preserved, the outer branch apparently with only two main forks. Inner gradate series represented by two separate crossveins, the anterior of which is well distad of the above-mentioned forks. Trichosors present. The colouration consists of brown mottles.

MATERIAL. In.43477 (H). Fig. 33.

REMARKS. The fragmentary specimen may well belong to *Hemerobius* but is too incomplete for its generic affinities to be ascertained. The species differs from *H. tinctus* sp. nov. in its larger size (the distance from the origin of the outer branch of Rs to the apical end of Sc is about 3.3 mm compared with 1.7 mm in *H. tinctus* sp. nov.) and position and incompleteness of the inner gradate series.

Species B

Fig. 32

DESCRIPTION. The species is known from a single body impression and forewing fragments. Head wide, with globular eyes and moniliform antennae. The abdominal sclerites are well preserved with a well-defined membranous area between the tergites and sternites, the modification of tergites 8-10 being indicative of a female (cf. Killington 1936 : fig. 13). Forewing: costal area moderately narrow, Rs apparently arising on more than one stem; outer branch of Rs with two main forks and two crossveins to R₁ a little distad of the forks. Trichosors present. The membrane is pigmented light brown in the pterostigmal area.

MATERIAL. In.17173 (S). Fig. 32.

DIMENSIONS. Length of body 4.0 mm.

REMARKS. The generic position of the species is uncertain, like Species A, but it is readily separated from the latter by the wing colour-pattern.

Species C

Fig. 34

DESCRIPTION. Dorsal impression of a fragment of a right forewing from near the base of the wing, maximum length 3.0 mm, width 1.5 mm. Sc on prominent upfold with the bases of eight oblique costal crossveins preserved. Stem of R slightly deflected posteriorly before converging on Sc basally; a transverse groove possibly represents a basal crossvein. Rs represented by four branches with fine parallel folds in the wing membrane between them. Some brownish pigmentation of the veins and membrane.

MATERIAL. In.17445 (B). Fig. 34.

REMARKS. Rs arising on several branches, the basal expansion of the subcostal area and general appearance of the fragment would place it in the Hemerobiidae (cf. corresponding area in Fig. 39, p. 258). The generic affinities of the fragment are indeterminate but size comparison with ? *Neuronema* sp. A indicates a species with probable wing length of about or a little less than two-thirds of the latter.

Family **CHRYSOPIDAE**
Subfamily **CHRYSOPINAE**

Species A

Fig. 42

DESCRIPTION. Dorsal impression of an apical fragment of a right hindwing, maximum width

3.1 mm, length 5 mm. Estimated original length 13–16 mm. Wing membranous; apex pointed, relatively sharp. Macrotrichial bases visible on wing margin and veins, especially numerous along C. Sc marked by prominent fold; Sc and R_1 curved towards apex distally. Rs zigzagged, with eight branches preserved, the basal four showing end-twigging. Rs linked to R_1 by a number of crossveins; branches of Rs joined by two series of gradate crossveins.

MATERIAL. I.8643 (B). Fig. 42.

REMARKS. R_1 distinct from Rs but linked by numerous crossveins, branches of Rs arising from a single (zigzagged) stem and the absence of trichosors are characteristic of Chrysopidae (Fraser 1959 : 15; Riek 1970 : 482). The reduced venation excludes the fossil from the Apochrysinæ (cf. Kimmins 1952) and places it in the Chrysopinæ in the wider sense (Riek 1970). The specimen is too fragmentary for more detailed determination. A Recent wing is illustrated in Fig. 41 for general comparison.

Recent chrysopids (green lacewings, etc.) are found in both warm and temperate regions of the world (Tjeder 1966 : 243). The larvae and adults (Chrysopinæ *s. lat.*) are predominantly arboreal although they also occur on low vegetation, where the larvae and many of the adults prey on small, soft-bodied arthropods, mainly insects (Balduf 1939 : 271–272, 291; Tjeder 1966 : 228).

Family SISYRIDAE

Species A

Fig. 27

DESCRIPTION. The species is known from a single left forewing, estimated original length 5.0 mm. The wing has been folded longitudinally in two upon itself, but the two halves are readily distinguished by (a) the general orientation of the veins and (b) the veins of the anterior portion being convex and ridge-like and the posterior ones concave since they are seen from the underside. Costal area moderately wide, macrotrichial bases visible along the anterior margin and on some crossveins. Sc curved towards R_1 apically, costal crossveins numerous, unforked. R forked near wing base, R_1 parallel to Sc basally but not preserved apically. Rs branching four times with R_2 apparently divided. Short inner gradate series of crossveins present and traces of an outer series. MA and MP divided apically, branches forked. CuA with seven short distal branches, the latter simple except for one which appears to be forked. CuA linked by prominent crossveins to CuP basally and MP apically. Colouration: veins and pterostigmal area light brown. The membrane shows traces of a similar pigmentation in the middle and outer parts of the wing.

MATERIAL. In.17287 (S). Fig. 27.

REMARKS. The wing form and venation of the fossil are closest to the extant genus *Sisyra* Burmeister (Fig. 28); Sc curving to terminate on R_1 distally is typically sisyrid (Nakahara 1958). The inner gradate series resembles that of *Sisyra panama* Parfin & Gurney and the fork of R_2 is similar to *S. vicaria* (Walker). Comparison with Recent species in the BM(NH) shows that the fossil differs from *Sisyra* in that the costal crossveins and branches of CuA are more numerous and the apical r_1 –rs crossvein appears to be immediately below rather than beyond the termination of Sc. The branching of CuA is more like the Nearctic sisyrid *Climacia areolaris* (Hagen) and the costal crossveins resemble *Neurorthus* spp. The Neurorthinae have been removed from the Sisyridae in recent years and elevated to family rank (Zwick 1967). The larvae of both families live in fresh water except those of *Austroneurorthus* Nakahara which probably inhabit damp places; adults are found near the larval habitat. The Sisyridae have a cosmopolitan distribution and the larvae are parasitic on fresh-water sponges (Porifera : Spongillidae) (Parfin & Gurney 1956; Zwick 1967; Riek 1970). Both neurorthids and sisyrids are known in the Baltic amber and a number of specimens await description (Macleod 1970). The systematic position of the amber 'sisyrid' *Rophalis relicta* Hagen is unsettled (Parfin & Gurney 1956; Nakahara 1958).

Family Uncertain

In.20557 (B). Fragment probably of the costal area of a wing, preserving a straight portion of the wing margin and distal parts of 22 crossveins. Length 5 mm, width 1 mm. Crossveins slightly inclined to the margin, evenly spaced, and single except for one with a terminal fork. Macrotrichial bases dense on wing margin and also evident along the veins, no trichosors. Membrane pale brown, veins and margin dark brown.

Order MECOPTERA
Suborder EUMECOPTERA
Family BITTACIDAE

Genus *BITTACUS* Latreille, 1805

TYPE SPECIES. *Panorpa italica* Müller 1766, by subsequent designation; Recent, western Palaearctic.

Bittacus veternus (Cockerell) comb. nov.
Figs 36, 44

1921*b* *Panorpa veterna* Cockerell : 478; fig. 47.

EMENDED DESCRIPTION. The species is known from the apical part of a right wing, original length estimated at 12–14 mm. Wing membranous, slightly folded about R_5 . Macrotrichia visible along part of anterior and posterolateral margins. R_1 represented by the curved apical end; R_s four-branched, R_{4+5} forking 4 mm from wing apex, R_{2+3} opposite the end of R_1 . R_{3-5} linked to each other by two transverse crossveins. M four-branched, M_{1+2} forking a little nearer the apex than R_{4+5} ; M_3 and M_4 converging but fork not preserved. First $r-m$ oblique, originating close to the base of R_5 ; 1st i.m. also oblique commencing near the end of the $r-m$ but is incompletely preserved. R_5 and M_{1-3} are also linked to each other by two transverse crossveins with one to M_4 . CuA represented by a small apical fragment. Wing colouration: veins brown; dark brown areas around the end of R_1 (pterostigma) and the transverse R crossveins; paler brown around the transverse M crossveins. Wing tip also dark. The pigmentation is similar in colour to Recent Mecoptera.

HOLOTYPE. In.24330, with counterpart (H). Figs 36, 44.

DIMENSIONS. Maximum width 3 mm, length 5 mm.

REMARKS. The reduced venation excludes the fossil from Meropeidae and Notiothaumidae (Grassé 1951 : 107) and places it in the Eumecoptera. Cockerell (1921*b*) stated that it resembles the living *Panorpa germanica* L. (Panorpidae) except in details of colour pattern. I have examined a series of specimens of this European species in the museum collection, and in addition the fossil differs in that R_2 is short and does not fork and that 1st $r-m$ is more or less continuous with 1st i.m. which is directed towards the anastomosis of M_{3+4} . In *P. germanica*, and *Panorpa* Linné in general, R_2 is usually forked (Carpenter 1931 : 213) although there are exceptions. Comparison of *P. germanica* with other panorpid species, e.g. in Esben-Petersen (1921), suggests that 1st i.m. is not normally present close to 1st $r-m$ and fork M_{3+4} is more basal in Panorpidae.

The venation of the fossil in fact agrees best with that of the Bittacidae (Esben-Petersen 1921 : 115–162), and I have compared the specimen with published accounts of the type species of the 12 currently recognized bittacid genera, as well as some additional species in the larger genera (*Bittacus*, *Harpobittacus* Gerstaecker). The shape and venation compares well with *Austrobittacus* Riek, *Bittacus* (e.g. *B. sinensis* Walker, Fig. 43), *Kalobittacus* Esben-Petersen, and possibly *Tythobittacus* Smithers. The absence of pterostigmal crossveins in the fossil could be preservational failure, as these may be faint in Recent specimens, and are sometimes obscure (Esben-Petersen 1921 : 127). The size corresponds to more than one of these genera: in *Bittacus* a Baltic amber species, *B. minutus* Carpenter, has wings of 3×11.5 –13 mm. The Bembridge Marls species approaches the living *B. marginatus* Mikayé in the pigmentation of the pterostigma, apex and more apical crossveins, and is provisionally referred to the genus *Bittacus* Latreille.

Recent bittacids (hanging flies) are found on vegetation in sheltered places and are predacious on other insects. The larvae are ground-dwelling scavengers, pupating beneath the surface (Grassé 1951; Byers 1971). The family is temperate-tropical (Carpenter 1931 : 206) with a world-wide distribution except for the northern parts of Europe, Asia and America (Esben-Petersen 1921 : 116). It is no longer found in Britain (Fraser 1959) although represented on the continent (Grassé 1951).

Bittacus sp. A

Fig. 46

DESCRIPTION. The species is known from a single ventral impression of an incomplete left wing without counterpart, of which pieces have flaked away and are not preserved. Original length estimated at *c.* 15 mm. The anterior and posterior margins are sufficiently well preserved to indicate a narrow elongate wing. The longitudinal veins are distinct, but some of the crossveins cannot be discerned although their positions are indicated by the undulations in R and M. R₁, R₅ and CuA are on prominent upfolds. Sc is close to anterior margin in the basal part of the wing, continuing beyond the fork of Rs. R₁ curved posteriorly at its distal end bounding the pterostigma on its posterior side. No definite traces of pterostigmal crossveins. Rs forking just basad of M, the former four-branched and the latter with only three branches preserved. R₃-M₃ interlinked by well-spaced crossveins; 1st i.m. oblique and well distad of the termination of CuP on the posterior margin. Wing colouration: veins brown, pterostigma dark brown; a slightly lighter brown area between R₁ and Rs immediately beneath and distad of pterostigma.

MATERIAL. In.64537 (H). Fig. 46.

DIMENSIONS. Maximum length 6.5 mm, width 1 mm.

REMARKS. The elongate form and well-developed pterostigma are typically bittacid (cf. Setty 1940 : 282). The venation is close to that of *Bittacus veterinus* (Cockerell) comb. nov. but it differs from the latter in that the pigmentation is confined to the pterostigma and adjacent membrane. The wing details agree with Recent *Bittacus* (Fig. 45), but in the absence of further information on this species it can only be referred to this genus in the wider sense.

Order LEPIDOPTERA
Suborder ZEUGLOPTERA
Family MICROPTERIGIDAE

Genus *MICROPTERIX* Hübner, 1825

TYPE SPECIES. *Tinea podevinella* Hübner 1813, by subsequent designation; Recent, western Palaearctic.

Micropterix anglica sp. nov.

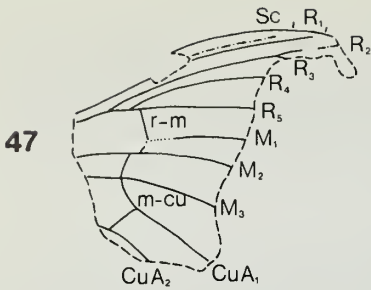
Fig. 49

DIAGNOSIS. A Palaeogene species of *Micropterix* with Sc forking distally beyond the origin of R₁ and R₁ unbranched in the forewing.

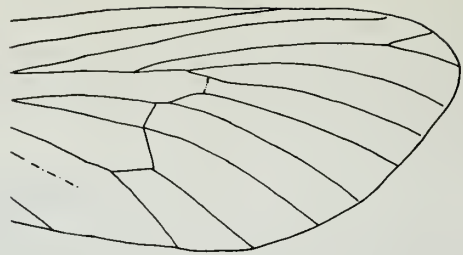
DESCRIPTION. The single known specimen consists of the greater part of a forewing, original length estimated at about 4 mm. Sc forked, R₁ simple. R₂ and R₃ originating from the outer half of the areole, chorda faintly preserved. R₄ and R₅ single, and like M₁, converging on the apical end of the areole; forks of M₂₊₃ and CuA₁₊₂ approximately beneath the basal end of the areole. CuP single. 1A represented by a short distal portion. Crossvein r-m faint but no trace of sc-r nor m-cu. Colouration: veins mostly dark brown with intervening membrane light brown.

HOLOTYPE. In.17411 (S). Fig. 49.

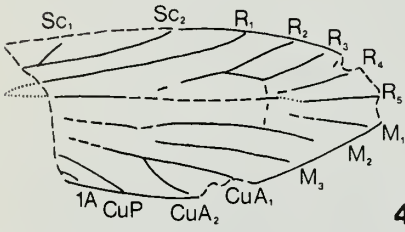
DIMENSIONS. Forewing: preserved length 2.4 mm, width 1.1 mm; length of Sc₂ 0.93 mm.



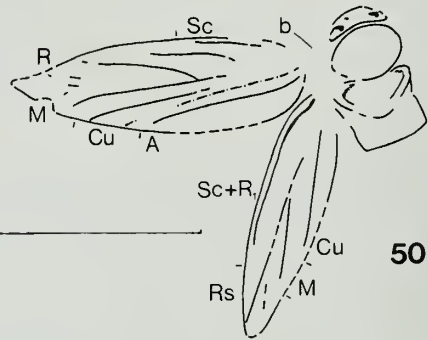
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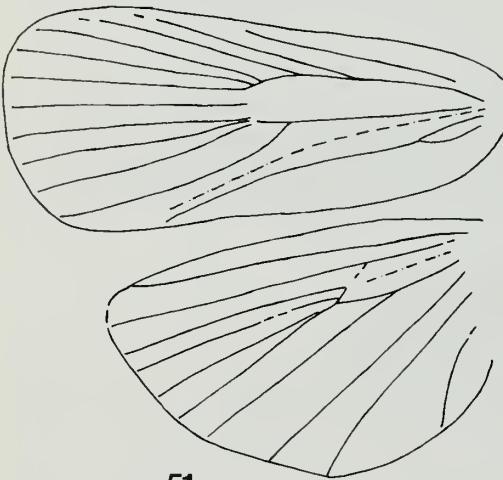
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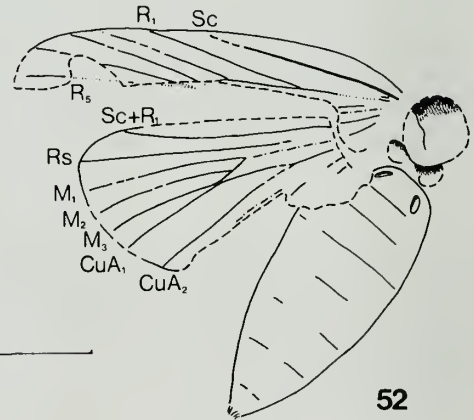
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50



51



52

Fig. 47 *Prohepialus* sp. Composite drawing of wing In.64528 (i-iii).

Fig. 48 *Hepialus fusconebulosa* (De Geer). Recent, Britain. Outer part of forewing.

Fig. 49 *Micropterix anglica* sp. nov. **Holotype**, In.17411.

Fig. 50 Microlepidoptera family uncertain sp. A, I.9492. (b = bristle).

Fig. 51 *Copromorpha gypsota* Meyrick. Recent, Fiji. Wing venation.

Fig. 52 *Copromorpha fossilis* sp. nov. **Holotype**, In.25766.

(Scale line = 2 mm. Figs 51-52 are to same scale.)

REMARKS. The homoneurous type of venation and vein details agree with the extant genus *Micropterix*. The absence of crossveins sc-r and m-cu is probably due to preservational failure, as they may be weakly developed in Recent micropterigids. The fossil differs from '*Micropterix*' *proavitella* Rebel (Baltic amber) in that Sc forks more apically and R₁ is unbranched (cf. Rebel 1935 : fig. 17). It approaches the Recent British species *Micropterix* [= *Eriocephala*] *cathella* (Linné) but differs principally in that Sc₁ is shorter and appears to originate more apically of the origin of R₁ compared with the latter (cf. Meyrick 1928 : figure on p. 873).

Recent micropterigids have a widespread distribution but *Micropterix* is confined to the Palaearctic Region. This primitive family includes the earliest known Lepidoptera, from the Lower Cretaceous of Lebanon (Whalley 1977). They are small, metallic-coloured, largely diurnal moths with functional mandibles and no proboscis, feeding on pollen grains; the larvae are considered to feed on bryophytes but some may be detritus feeders (Common 1970). Adult *Micropterix* visit blossoms including *Carex* L. and *Ranunculus* L., both genera being represented in the Insect Bed.

Suborder **EXOPORIA**
Superfamily **HEPIALOIDEA**
Family **HEPIALIDAE**

Genus *PROHEPIALUS* Piton, 1940

TYPE SPECIES. *Prohepialus incertus* Piton 1940, by monotypy; Palaeocene, Menat (Puy-de-Dôme).

Prohepialus sp.
Figs 38, 47, 59

1976 hepialid, Jarzembowski : 13.

1977 hepialid, Robinson : 108; figs 5–6.

DESCRIPTION. The material consists of four incomplete wings, estimated wing length 20–45 mm. Sc marked by prominent fold, close to R_1 distally and like R_1 continuing well beyond the end of the discal cell. R_{2+3} closer to R_4 than R_1 at base. Base of R_4 well separated from origin of r-m. Discal cell widening towards apex, M bifurcate in cell. The distance from posterior end i.m. to the anterior end r-m is 0.6 of width of the discal cell across apical angles. R_{2+3} forking beyond the cell at c. 1.3 of maximum width of the latter; M_1+r-m and CuA_1+m-cu form outwardly-directed angles from the apical end of the cell. Crossvein i.m. oblique, originating from the fork of M_{1+2} or a little basad of the fork. No colour pattern is preserved, but the wing surface has a brownish tinge in some of the specimens because of the presence of scales. In.64528(i) shows numerous oblong scales, but the counterparts, In.64528(ii–iii), show longer forms. Fold Sc is convex in the part indicating that this is the dorsal impression of the wing with scales from the same surface; the counterparts therefore show the ventral scales. Adpressed marginal scales can be seen in In.64528(iii) and In.64538+counterpart, the latter also with long scales on both surfaces.

MATERIAL. In.17464 (Fig. 38); In.64528(i) and fragments of counterpart In.64528(ii–iii) (Fig. 47); In.64538 (Fig. 59) and counterpart on reverse of In.64528(ii); In.64539 (H).

DIMENSIONS. Width of discal cell across apical angles 9.8–c. 4.4 mm (In.64538–9).

REMARKS. The general habitus of the wings is indicative of the Hepialoidea, and M forked in the discal cell, m-cu (M_1 *auctt.*) oblique, and comparatively large size place them in the Hepialidae, commonly known as swift moths (Common 1970 : 787, 789). Relationships with Recent genera are uncertain, but the *Hepialus*-like venation (cf. Fig. 48) agrees with the Palaeogene genus *Prohepialus* Piton. The latter genus is based on a single specimen of which the venational details are incompletely known, rendering specific comparison impossible.

The hindwings of *Hepialus* spp. are slightly smaller than the forewings and this would increase the total variation in wing size. In.64538 and In.64528 could be the fore- and hindwings of the same individual as they come from the same piece of rock, both show traces of pigmented scales, and the difference in size of the discal cell (apical width differs by c. 33%) is within the range of some Recent hepialid specimens. Examination of both surfaces of the forewing of the Recent British *Hepialus fusconebulosa* (De Geer) (Fig. 48) showed a similar shape difference in the scales as in In.64528, and the presence of long scales in the hindwing as in In.64538+counterpart. The presence of broad longitudinal ridges as well as more numerous, finer ridges is a feature of hepialid scales that was noted by early workers (e.g. Kellogg 1894 : 80–82); both types of

longitudinal ridge and other ultrastructural details are preserved in the scale shown in Fig. 59.

The family has a cosmopolitan distribution but is most diverse in the southern hemisphere. The larvae are phytophagous, tunnelling in wood or soil; the adults are short-lived with mouthparts more or less reduced and functionless (Bourgogne 1951 : 372; Common 1970 : 787).

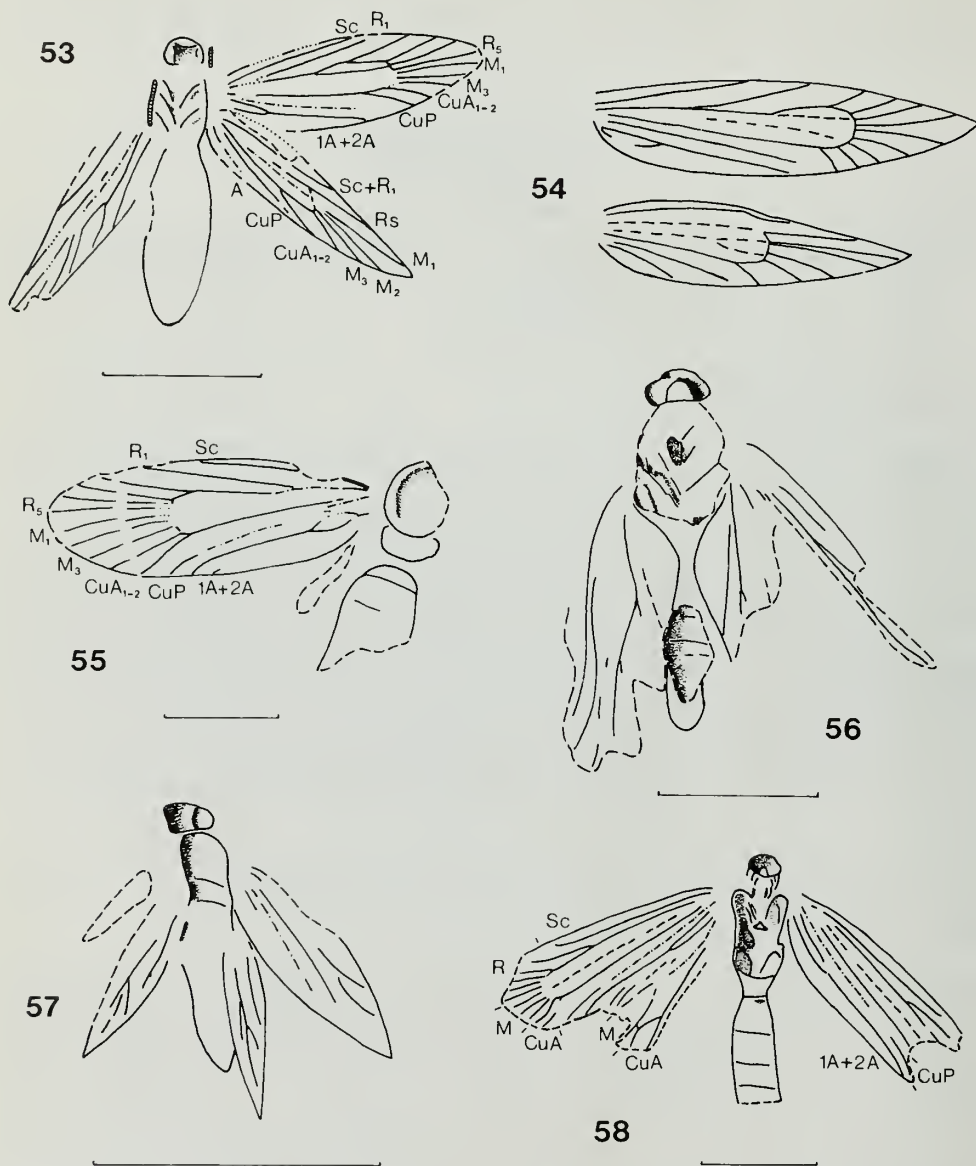


Fig. 53 *Paratriaxomasia solentensis* gen. et sp. nov. **Holotype**, 1.9166.

Fig. 54 *Triaxomasia caprimulgella* (Stainton). Recent, Europe. Wing venation, after Zagulyaev (1964).

Fig. 55 Tineidae species A. 1.9614.

Fig. 56 Gelechioidea species A. 1.9042.

Figs 57-58 Microlepidoptera family uncertain. Fig. 57, species C. In.25512 + In.25252. Fig. 58, species K. In.25219.

(Scale line = 2 mm)

Suborder **DITRYZIA**
 Superfamily **TINEOIDEA**
 Family **TINEIDAE**

Genus **PARATRIAXOMASIA** nov.

DIAGNOSIS. A Palaeogene genus of Tineidae approaching the extant genus *Triaxomasia* Zagulyaev but differing in that the forewing is slightly broader and the hindwing lacks a marginal indentation near the termination of Sc+R₁ and is slightly narrower towards base.

TYPE SPECIES. *Paratriaxomasia solentensis* gen. et sp. nov.

Paratriaxomasia solentensis gen. et sp. nov.

Fig. 53

DIAGNOSIS. Species of *Paratriaxomasia* with a forewing span of 8.0 mm.

DESCRIPTION. The species is known from a single ventral impression of the body and wings. Head rounded anteriorly. Forewing approximately three times as long as broad, attenuated apically. Sc close to anterior margin-terminating opposite the origin of R₂. R₁ originating a short distance from wing base at about 0.25 of the length of the discal cell. Areole elongate, 0.4 of the

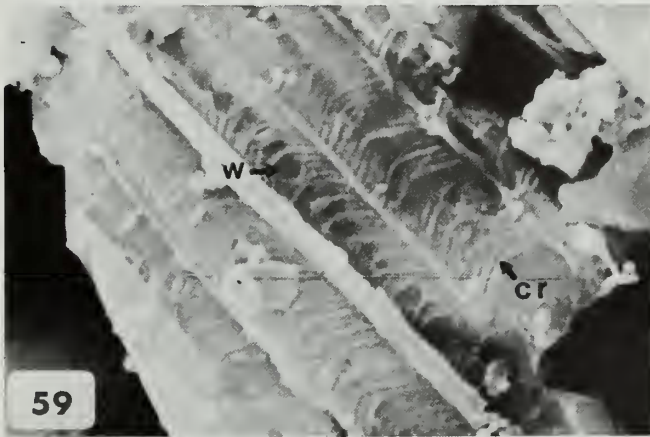


Fig. 59 *Prohepialus* sp., In.64538 (scale, $\times 10\ 000$; lr longitudinal ridge, cr cross rib, w window).

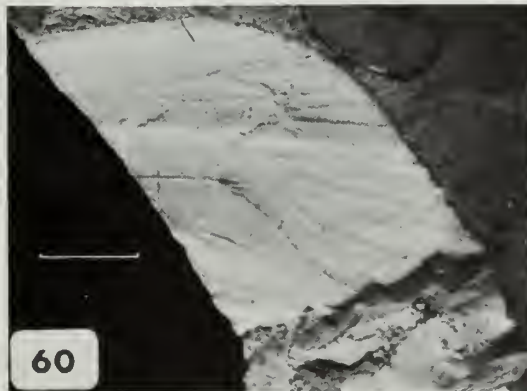


Fig. 60 *Gurnetia durranti* Cockerell, holotype. In.24324. See also Fig. 66. (Scale line = 2 mm)

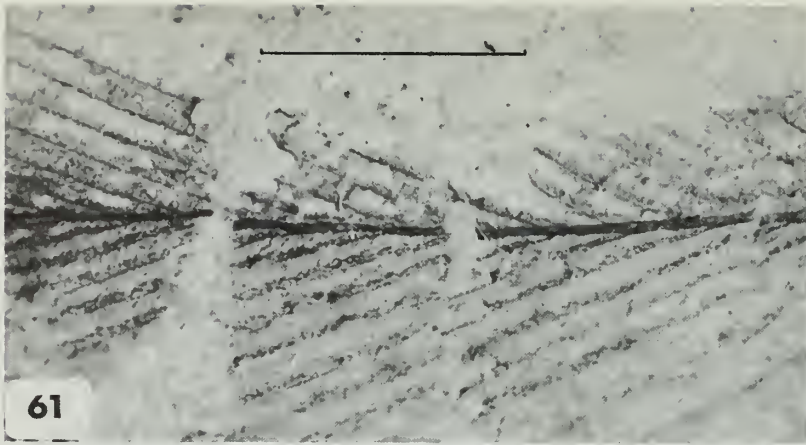


Fig. 61 Fragment of small bird feather, occurring on slab In.17194. See p. 239. (Scale line = 2 mm)

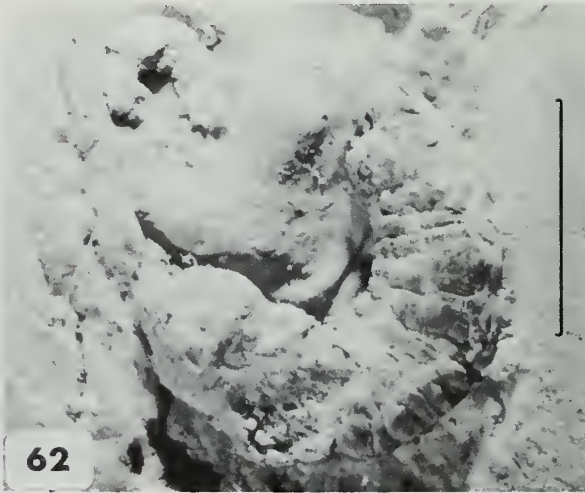


Fig. 62 Insect larvae inside cavity of a plant stem. In.64544. See p. 241. (Scale line = 2 mm)

cell length; R_3 – R_5 , M_1 – M_3 and CuA_1 – CuA_2 originating from the apical part of the cell, the origin of R_2 basad of that of CuA_2 . R_5 appears to terminate immediately anterior to the wing apex. Hindwing lanceolate, 4.5 times longer than broad and gradually tapering towards the apex. $Sc + R_1$ well separated from the anterior margin, terminating at midlength of wing opposite the apical end of the discal cell. M_1 towards apex, converging on M_2 basally and continuing as a fold into the discal cell. M_3 originating close to M_2 and CuA_1 . CuP prominent, anal vein present. Stem of CuA well separated from the posterior margin.

HOLOTYPE. I.9166 (B). Fig. 53.

DIMENSIONS. Length of body 3.6 mm, forewing 3.6 mm and hindwing 3.3 mm.

REMARKS. The wings resemble those of the extant monotypic genus *Triaxomasia* (Fig. 54), from which they differ in that the forewing is slightly broader, there is no faint trace of M in the discal cell and the chorda and $2A$ appear to be stronger veins; the hindwing is narrower basally, and there is no shallow indentation on the anterior margin near the distal end of $Sc + R_1$ as in

Triaxomera Zagulyaev. The forewing span of the European *Triaxomasia caprimulgella* (Stainton) (Fig. 54) is 10·5–11·5 mm, and like other Nemapogoninae, it is a forest dweller and the larvae are fungus feeders. The caterpillars of this species inhabit fungus-infested rotten wood including *Fagus* L., *Ulmus* L. and *Quercus* L. (Zagulyaev 1964 : 86, 133, 155–160).

Genus *indet.*

Species A

Fig. 55

DESCRIPTION. The species is known from a single specimen with thorax, basal part of abdomen and a single forewing preserved. Meso- and metathorax distinct. Forewing elongate, about three times as long as broad, apex bluntly angular; membrane with distinct transverse lineation. Discal cell elongate, 0·6 of wing length. Sc close to anterior margin, terminating near middle of wing. R_1 originating at a quarter of wing length from base, terminating a short distance beyond the apical end of the discal cell. Branches of R, M and CuA originating relatively close to each other, R_5 towards apex; origin of R_2 a little more basad in position than that of CuA_2 and marking an anterior deflection in the stem of R. Discocellular crossveins indistinct. Chorda apparently absent, but preservational failure in the discocellulars raises the possibility that a weak chorda was present in life. 1A+2A with a short basal loop and well separated from the posterior margin.

MATERIAL. I.9614 (B). Fig. 55.

DIMENSIONS. Length of thorax 1·8 mm. Length of forewing 5·8 mm, maximum width of forewing 2·0 mm.

REMARKS. The forewing bears some resemblance to that of the incurvariine *Adela reamurella* (Linné) but differs notably in that the apex is more rounded and there is a wider area between the apical end of the discal cell and the outer margin (cf. Meyrick 1928 : figure on p. 843). It is similar in size and form to *Tinea pellationella* (Linné) (cf. Forbes 1923 : fig. 73) although in the latter the forewing is more elongate (about four times as long as broad) and a chorda is present. The venation is also close to that of *Nemapogon granella* (L.) in which the chorda is faint (Forbes 1923 : fig. 74, *Tinea granella* (L.)) and the fossil apparently belongs in the Tineidae, a widespread present-day family.

Superfamily GELECHIOIDEA

Species A

Fig. 56

DESCRIPTION. The single specimen consists of a ventral impression of the body, incomplete hindwings and part of the right forewing. The last shows portions of Sc and R, the latter with two well-spaced branches. Hindwing: moderately wide, Sc+ R_1 and Rs sinuous and preserved in the left wing only; CuA preserved in both wings, CuP prominent, anal area broad, angular.

MATERIAL. I.9042 (B). Fig. 56.

DIMENSIONS. Length of body 4·5 mm.

REMARKS. Although the fossil is rather fragmentary, the hindwing form and venation resemble some extant gelechiids including *Agnippe* sp. (Brues, Melander & Carpenter 1954: fig. 421), *Parachronistis albiceps* (Zeller) (Spuler 1913 : fig. 123) and *Polyhymno luteostrigella* Chambers (Forbes 1923 : 256). It is tentatively referred to the Gelechioidea. The superfamily has a cosmopolitan distribution; the larvae are usually phytophagous.

Superfamily COPROMORPHOIDEA

Family COPROMORPHIDAE

Genus *COPROMORPHA* Meyrick, 1886

TYPE SPECIES. *Copromorpha gypsota* Meyrick 1886, by monotypy; Recent, Australian Region (Pacific).

Copromorpha fossilis sp. nov.

Fig. 52

DIAGNOSIS. A Palaeogene species differing from the living *C. gypsota* in the smaller size of the wings, the slightly more basad termination of the branches of R in the forewing, and M_1 closer to Rs in the hindwing.

DESCRIPTION. The single specimen consists of the dorsal impression of a decapitated body and the remains of the right wing pair.

Body: posterior end of mesothorax rounded, metascutum distinct. Abdomen completely flattened except for two lateral cavities in the basal segment; seven annuli are discernible and the remains of the apical scale cover. The abdomen is comparatively large even allowing for compression and, together with the pointed posterior, suggests that the holotype is a female.

Forewing: anterior margin rounded basally, straightening distad of the termination of Sc and curving strongly past R_4 . Sc terminating near the mid-length of the wing; R_1 originating at 0.25 and terminating at 0.65 of the forewing length (from base); R_3 and R_4 terminating at 0.85 and 0.94 of the same length. Base of R_2 well separated from that of R_1 . CuA, 1A and 2A represented by short basal portions close to the CuP fold; anal veins well separated from the margin.

Hindwing: apex rounded with an angle of 85° . Anterior margin straight, outer margin curving gently towards base away from the apex. Sc + R_1 elongate continuing apically well beyond the end of the discal cell. Rs directed towards apex. Bases of M_1 – M_3 linked by oblique crossveins. M_2 equidistant between M_1 and M_3 , M_1 continuing as a distinct fold in the discal cell. Base of M_3 touching CuA₁ at 0.4 of its length from the separation of CuA₂.

HOLOTYPE. In.25766 (H). Fig. 52.

DIMENSIONS. Length of forewing 8.8 mm.

REMARKS. The wing form and venation come closest to that of extant moths of the family Copromorphidae and the type genus itself (Fig. 51). The genitalia of Copromorphoids show affinities with those of the Gelechioidea and the venation of the fossil shows some resemblance to the Oecophoridae. Although the bases of R_4 and R_3 are not preserved, their courses indicate that they do not form a distinct fork as is characteristic of the Oecophoridae. The apical angle is close to 90° , in agreement with the Copromorphidae.

The family has a southern distribution, only *Aegidomorpha* Meyrick entering the Palaearctic in China; *Copromorpha* occurs in Africa and from India through to Australia. Copromorphid larvae are tunnellers in leaf veins, twigs and fruits (Common 1970 : 827).

Microlepidoptera, Family uncertain

Species A

Fig. 50

DESCRIPTION. The species is known from the dorsal impression of a single specimen with the left pair of wings and anterior part of the body preserved. Estimated wing span 6.0 mm. Body pale brown; base of abdomen, meso- and metathorax distinct but dorsoventrally compressed. Head rounded anteriorly. Wings elongate, apices pointed, with some scale traces.

Forewing: broader and slightly longer than hindwing. Anal area broad, CuP marked by a prominent fold terminating on the posterior margin at 0.6 of the wing length from base; Sc close

to anterior margin and terminating at 0·4 of the same length. Distal part of stem R + M preserved close to CuA; two branches of R well defined as in Fig. 50 and apical venation suggested by some faint traces. CuA and A single and close to CuP fold.

Hindwing: Sc + R₁ thickened basally, long and close to anterior margin: a detached bristle may represent the frenulum. Rs + M forking near mid-length of wing; Cu single.

MATERIAL. I.9492 (B). Fig. 50.

DIMENSIONS. Forewing length 2·7 mm; hindwing length 2·3 mm.

REMARKS. The venation approaches that of the modern leaf-miners *Heliozela* Herrich Schaffer (Common 1970 : fig. 36.15B) and *Nepticula* Heyden (*N. terminella* Braun ♀, Forbes 1923 : fig. 56), and Species A probably belongs in either the Incurvariina or Nannolepidoptera.

Species B

DESCRIPTION. The species is known from a single specimen consisting of the ventral impression of the body plus forewings. Estimated wing expanse 6·0 mm. Body elongate, head well rounded anteriorly. Forewing lanceolate, with some traces of scale cover. Sc close to but well separated from anterior margin, probably not continuing beyond mid-length of wing. Anal area broad, CuP fold prominent. Stem of R + M close to CuA; R producing three branches to the anterior margin in outer half of wing, some faint suggestions of venation posterior to last branch. Vein A single, and like the stem of CuA, close to CuP fold.

MATERIAL. In.64540 (H).

DIMENSIONS. Body length 2·8 mm, forewing length 2·7 mm.

REMARKS. The forewing venation comes close to that of *Heliozela* but also resembles the gelechioid *Dyselachista sericiella* (Haworth) [= *saltatricella* (Fischer von Röslerstamm)] (cf. Spuler 1913) and the lyonetiid *Leucoptera laburnella* (Stainton) (cf. Meyrick 1928); the exact affinities are uncertain. The latter two species are a little larger than Species B.

Species C

Fig. 57

DESCRIPTION. A very small moth with an estimated wing expanse of about 3·8 mm. Head rounded anteriorly. Mesothorax oval, scutellum short and pointed posteriorly; metascutum laterally lobate (In.17142).

Forewing: lanceolate, CuP fold prominent extending for 0·6 of wing length, CuA and A close to fold. Sc close to anterior margin, extending approximately to mid-length of wing. R represented by a distal fork. Anal area broad.

Hindwing: linear-lanceolate, with some well-preserved scales (In.25512 + 25252). Sc + R₁ well separated from the anterior margin and elongate like CuA; Rs + M apparently with three branches in outer part of wing.

MATERIAL. In.25512 (H) and counterpart In.25252 (H), both Fig. 57; In.17142 (S).

DIMENSIONS. Length of body 1·9 mm, forewing 1·7 mm.

REMARKS. Although rather small, the venation shows some resemblance to the extant lyonetiids *Leucoptera* Hübner and *Bedellia* Stainton; the species probably belongs in the Tineoidea.

Species D

DESCRIPTION. The single specimen consists of the abdomen and incomplete fore- and hindwings. The abdomen tapers to a point posteriorly and the specimen is probably ♀. The forewing is

represented by a median fragment and suggests an elongate wing with a discal cell; two oblique branches of R are preserved. A hindwing fragment shows the basal portions of M_3 and of both branches of CuA; M_3 originates very close to CuA_1 and is linked by a short crossvein.

MATERIAL. In.17392 (S).

DIMENSIONS. Length of abdomen 2.7 mm.

REMARKS. The general appearance of this fragmentary fossil is suggestive of the Ditrysia.

Species E

DESCRIPTION. A single dorsal impression of a body and basal half of a forewing. Head rounded anteriorly, thorax typically lepidopterous. Mesoscutellum 0.3 of the length of the mesothorax and rounded posteriorly with traces of the postnotum, suture with mesoscutum gently curved anteriorly; metascutum short with a narrow central portion between the meso- and meta-scutellum. Abdomen with some traces of segmentation.

Forewing: area between the stem of R and anterior margin moderately wide, Sc well separated from the margin. Base of R_1 closer to R_2 than Sc but well separated from the former. Discal cell moderately narrow. CuA, CuP fold and $1A + 2A$ close, the last apparently with a basal loop.

MATERIAL. In.25251 (H).

DIMENSIONS. Length of body 3.5 mm, abdomen 2.1 mm.

REMARKS. The affinities of this moth are uncertain but the general appearance suggests that it belongs to one of the 'tineoid' superfamilies.

Species F

DESCRIPTION. A single dorsal impression of the anterior part of the body and the remains of the left wing pair. Head rounded anteriorly. Scutoscuteellar suture of mesothorax curved anteriorly, scutellum small and truncate posteriorly. Metathorax elongate with a straight transverse suture with the mesothorax. Abdomen represented by two basal segments.

The wings consist of an incomplete hindwing overlying part of the forewing in which $1A + 2A$ and the basal loop can be discerned. The venation of the hindwing is more complete and suggests an elongate wing: Sc well separated from the anterior margin, CuA_1 and CuA_2 slightly divergent. M apparently arising on two branches, M_3 equidistant between M_{1+2} and CuA_1 . M_{1+2} relatively close to Rs , M_3 continuing into the discal cell. Discocellular crossveins present. Fine transverse lines and some scales are visible on the wing membrane.

MATERIAL. I.9783 (B).

DIMENSIONS. Length of thorax 1.5 mm.

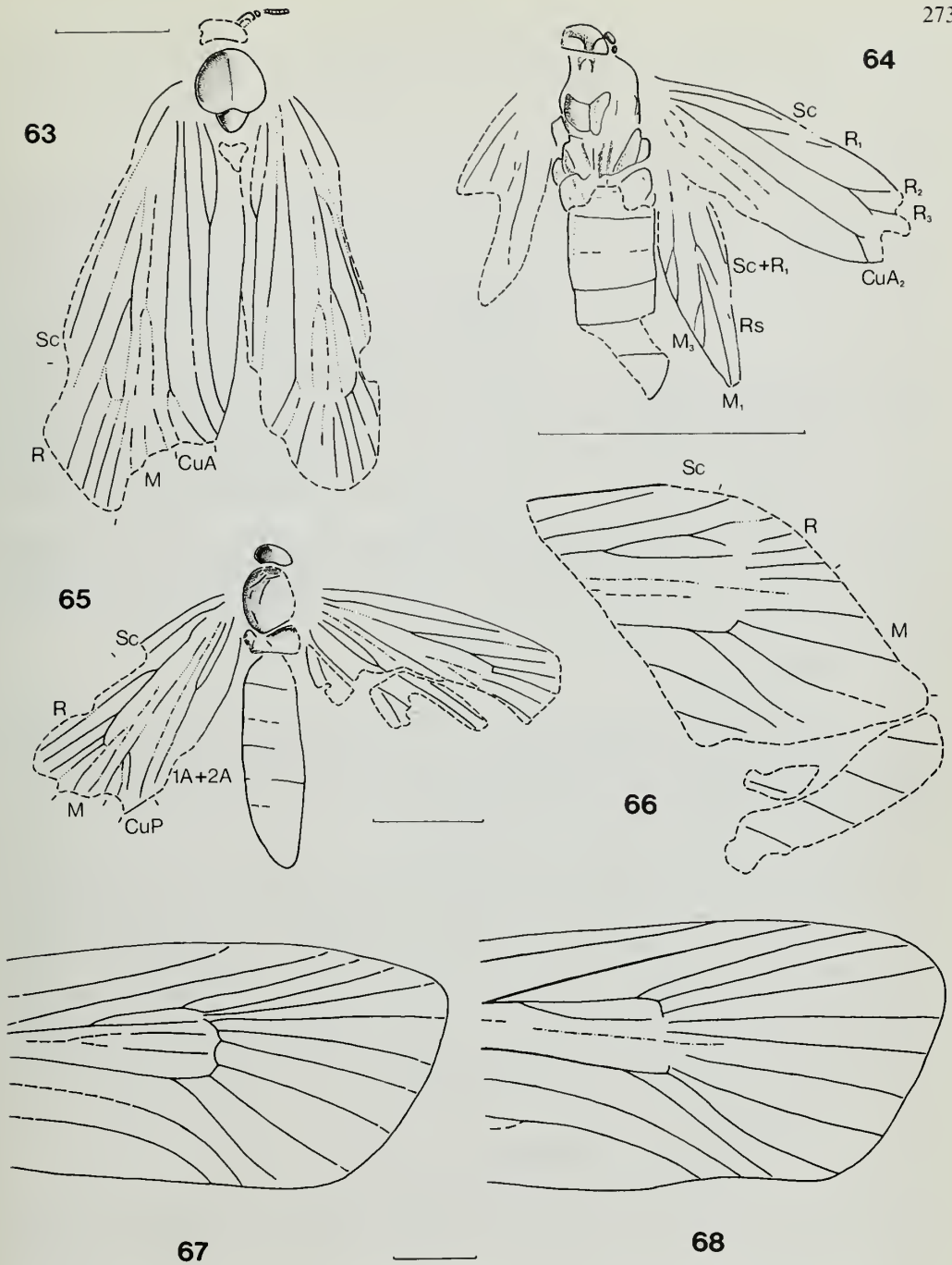
REMARKS. The affinities of this moth are uncertain: the hindwing venation shows some resemblance to *Adela ridingsella* Clemens (Incurvariidae) and *Haplotinea insectella* (Fabricius) (Tineidae).

Species G

Fig. 63

DESCRIPTION. A single dorsal mould of the anterior part of the body plus forewings. Antennae typically lepidopterous with pedicel larger than the flagellar segments and an expanded scape. Mesoscutellum pointed posteriorly, and markedly convex (in dorsal view) like the mesoscutum.

Forewings moderately broad and directed posteriorly as in rest position. Estimated original wing length 10.0 mm. Discal cell elongate with traces of M. R_1 originating at 0.35 from the base of the cell, R_2-R_4 from the posterior part of the areole, R_3 closer to R_4 . M_1-M_3 and CuA_1-CuA_2



Figs 63–65 Microlepidoptera family uncertain. Fig. 63, species G. I.8917. Fig. 64, species H. I.8809. Fig. 65, species L. In.24506 with details of head and right forewing from counterpart In.64543. Fig. 66 *Gurnetia durranti* Cockerell, holotype. In.24324. See also Fig. 60. Fig. 67 *Acrolophus* cf. *cossoides* Felder & Rogenhofer. Recent, Brazil. Outer part of forewing. Fig. 68 *Culama* sp. Recent, Australia (Meyrick coll. BM(NH) 1938–290). Outer part of forewing. (Scale line = 2 mm. Figs 66–68 same scale.)

originating close together from the apical end of the discal cell, the origin of CuA_2 less basad than that of R_1 . Fine transverse lines present on wing membrane.

MATERIAL. I.8917 (B). Fig. 63.

DIMENSIONS. Length of discal cell in forewing 5.6 mm.

REMARKS. The form of the thorax and primitive venation are very close to that of the tineid genus *Acrolophus* Poëy (cf. Forbes 1923 : fig. 19) but also to the incurvariine *Adela* Latreille (cf. Spuler 1913 : fig. 223).

Species H

Fig. 64

DESCRIPTION. A single ventral impression of the body with wing remains. Head rounded anteriorly. Estimated forewing span 5–6 mm.

Forewing: discal cell elongate and moderately narrow. Sc close to anterior margin and apparently terminating in basal half of wing. R_1 short, originating at 0.3 of the length of the discal cell from base. R_2 and R_3 originating from the apical end of the cell, bases well separated. Only a single branch of CuA is preserved, the base opposite that of R_3 . CuP fold slightly closer to CuA than A.

Hindwing: elongate, wing tip attenuate. Sc + R_1 close to anterior margin. Rs + M forking near mid-point of wing, M forking a short distance apically; Rs to the outer part of the anterior margin, M_1 – M_3 to the outer part of the posterior margin, M_2 and M_3 with common stem. CuA forking opposite Rs + M, branches short.

MATERIAL. I.8809 (B). Fig. 64.

DIMENSIONS. Length of discal cell in forewing c. 2.0 mm.

REMARKS. The fossil's venation shows some resemblance to that of the gracillariid *Caloptilia alchimiella* (Scopoli) (cf. Meyrick 1928 : figure on p. 788) and some small gelechioids, and it apparently belongs amongst the 'tineoid' superfamilies.

Species I

DESCRIPTION. A single specimen, the body being represented by the abdomen, parts of the thorax and a single leg, all of which are crushed. Estimated forewing span 11–12 mm. Hindwing represented by a median fragment indicating a broad wing, with part of CuA and M_3 preserved. Forewing elongate, over 3.5 times as long as broad, apex unknown. Discal cell relatively narrow, oblique. R_1 originating at 0.45 of the length of the discal cell from base, a short distance basad of the termination of Sc. R_2 – R_5 , M_1 – M_3 and CuA_1 – CuA_2 apparently all present and originating from the apical part of the cell, base of R_3 nearly opposite that of CuA_2 . 1A + 2A with basal loop. Forewing covered with numerous well-preserved scales.

MATERIAL. In.64541 (E. A. Jarzembowski & Tertiary Research Group, London). Sticelett Ledge.

DIMENSIONS. Length of discal cell in forewing 3.2 mm, of abdomen 2.8 mm.

REMARKS. The venation resembles extant species of *Gelechia* Hübner, *Plutella* Schrank (cf. Forbes 1923) and *Stegasta* Meyrick; the fossil apparently belongs in one of the 'tineoid' superfamilies.

Species J

DESCRIPTION. A single fragmentary specimen consisting of the thorax and incomplete fore- and hindwings. Forewing elongate, stem of A and CuA close to prominent CuP fold. R with three–four branches preserved in outer half of wing. Sc apparently terminating on anterior margin a little distad of the origin of R_1 . Hindwing venation too poorly preserved for comment.

MATERIAL. In.25157 (H).

DIMENSIONS. Length of forewing 3.4 mm.

Species K

Fig. 58

DESCRIPTION. A single ventral impression of the head, thorax and basal part of abdomen with remains of fore- and hindwings. Body elongate, wing membrane with a faint transverse lineation.

Forewing: discal cell elongate with traces of M. Venation complete, R_2 - CuA_2 originating from the apical end of the discal cell. Base of R_1 well separated from that of R_2 , Sc terminating on anterior margin a short distance beyond the base of R_1 .

Hindwing: an incomplete left wing is preserved, anteriorly overlapping the posterior part of the corresponding forewing. Sc + R_1 and Rs represented by two short distal fragments. M forking in the discal cell. M_3 linked to CuA_1 by a short crossvein.

MATERIAL. In.25219 (H). Fig. 58.

DIMENSIONS. Length of discal cell in forewing 3.1 mm.

REMARKS. The general habitus is indicative of the 'tineoid' superfamilies and the fossil resembles the extant yponomeutid *Plutella annulatella* (Curtis) (Forbes 1923 : fig. 200), but its exact systematic position is unknown.

Species L

Fig. 65

DESCRIPTION. A single specimen with body, both forewings and fragments of left hindwing. Mesothorax oval with apparent traces of the reduced prothorax anteriorly (In.24506); metascutum short and laterally expanded. Wing membrane with transverse lineation.

Forewing: broad, discal cell elongate with traces of M. R with four branches. R_1 originating at 0.5 of the length of the discal cell from base. R_2 closer to R_3 than to R_1 but well separated from the former. Sc well separated from the anterior margin terminating on the latter just beyond the base of R_2 . R_{4+5} , M_{1-3} and CuA_{1-2} originating closely from the apical end of the discal cell, CuA_2 opposite R_3 . Fork of $1A+2A$ well separated from posterior margin of wing.

Hindwing: two fragments with vein traces probably of Rs, M, CuA and A.

MATERIAL. In.24506 (H) and counterpart In.64543. Fig. 65.

DIMENSIONS. Length of body 5.8 mm, length of discal cell in forewing 3.2 mm.

REMARKS. The venation resembles that of the extant psychid *Lypusa maurella* (Denis & Schiffermüller) although there is some trace of a chorda in the forewing of the latter (cf. Spuler 1913 : fig. 206). The fossil probably belongs in the Tineoidea.

? Superfamily COSSOIDEA

? Family COSSIDAE

Genus *GURNETIA* Cockerell, 1921

TYPE SPECIES. *Gurnetia durranti* Cockerell 1921, by monotypy.

Gurnetia durranti Cockerell, 1921

Figs. 60, 66

1921b *Gurnetia durranti* Cockerell : 473; fig. 38.

HOLOTYPE. In.24324 (H). Figs 60, 66.

DIMENSIONS. Forewing (incomplete) : maximum length 9.4 mm, width 6.5 mm.

REMARKS. The genus and species is known from a single incomplete forewing with associated fragments probably of the hindwing. Estimated original length of forewing 15 mm. The transverse lineation on the membrane (Fig. 60) readily excludes it from the trichopteran family Limnephilidae (cf. Cockerell 1921*b*). Cockerell and Durrant (Cockerell 1921*b*) placed *Gurnetia* in the Cossidae and comparison with Recent material shows that the venation is close to that of the Australian genus *Culama* Walker (Fig. 68). The primitive type of venation shown by *Gurnetia* is also developed in certain microlepidoptera. Cockerell commented on the resemblance to the incurvariine *Nemophora* Hoffmannsegg, but the forewing of this is only about 6–8 mm long. CuA_2 originating close to CuA_1 near the apical end of the discal cell readily excludes the fossil from the Tortricidae. However, the fossil's venation does approach certain genera in the 'tineoid' superfamilies, a possibility not discussed by Cockerell and Durrant (*ibid.*). Thus it resembles the yponomeutid *Orthotaelia sparganella* (Thunberg) which has a maximum forewing length of 13 mm, although the posterior part of the wing is narrower in the latter. It also resembles the extant New World genus *Acrolophus* (Fig. 67), in which wing spans of 30–40 mm are often attained. The placement of *Gurnetia* in the Cossoidea is therefore uncertain although it undoubtedly belongs to the lower Ditrysia.

Superfamily PYRALOIDEA

Family PYRALIDAE

Subfamily PYRALINAE

Genus *PYRALITES* Heer, 1856

TYPE SPECIES. *Pyralites obscurus* Heer 1856, by monotypy; Oligocene, Aix-en-Provence.

Pyralites preecei sp. nov.

Fig. 69

DESCRIPTION. Single specimen consisting of decapitated body in dorsal aspect and remains of both fore- and hindwings. Mesothorax oval, scutellum rhomboidal, 0.4 of mesothoracic length. Left tegula distinct. Metascutum typically lepidopterous with two lateral lobes. Abdomen compressed but with some pink calcareous infill showing a number of fine tubular structures. The segmentation of the abdomen is obscure except for the more sclerotized basal segment.

The left wings are partly overlapping, but details of the hindwing venation can be seen beneath the forewing where the posterior part of the latter has flaked away. No trace of colour except some pale brownish pigmentation of the veins; scaly areas may be locally discernible on the membrane.

Forewing: discal cell long and narrow with traces of a median fold. Sc close to anterior margin continuing beyond the end of the discal cell. R producing three branches in outer half of cell, the second branch originating a little nearer the third than R_1 . The branches of R and Sc run closely and very obliquely towards the anterior margin but their terminations are not preserved. M_{1-3} curving towards outer margin, M_1 forming an angular fork with the third branch of R, and M_2 originating near to M_3 . CuA_1 and CuA_2 diverging from the cell less obliquely than Sc and R branches, CuA_2 separating about midway between R_1 and the second branch of R. The venation suggests a relatively narrow forewing with original length estimated at 15 mm.

Hindwing: anterior margin obscure, discal cell much shorter and broader than in forewing. Sc + R_1 prominent, close to Rs for a short distance in distal part of its course. Rs indistinct

Fig. 69 *Pyralites preecei* sp. nov. Holotype, I.8640. Body and left wing pair.

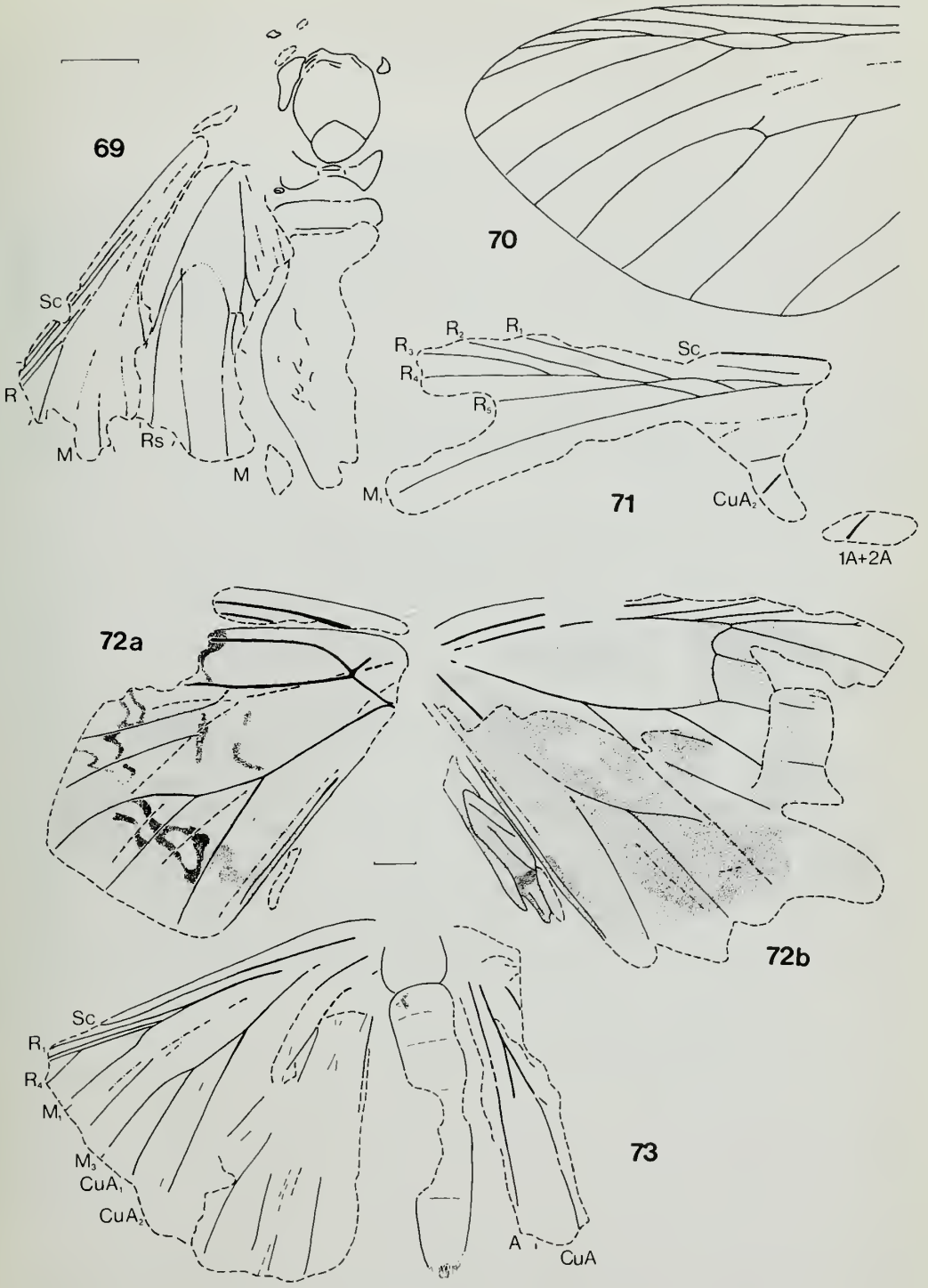
Fig. 70 *Chloroclysta truncata* (Hufnagel). Recent, Britain. Outer part of forewing.

Fig. 71 *Geometridites larentiiformis* sp. nov. Holotype, I.8866 and I.8935 (composite drawing).

Fig. 72 *Nymphalites zeuseri* sp. nov. Holotype, Fig. 72a, part I.10384; Fig. 72b, counterpart I.10384a. See also Figs 75–76.

Fig. 73 ? Papilionoid, In.64545a.

(Scale line = 2 mm. Figs 69–71 same scale; Figs 72–73 same scale.)



inwards of the fork with M_1 . Bases of M_2 , M_3 and CuA_1 closely spaced, apparently linked by crossveins. Only the ends of mdc are preserved, indicating a strong asymmetric basal arch.

The right wings are preserved at an angle of $c. 15^\circ$ to the plane of the body, inclined downward and slightly overlapping the abdomen on the same side. They show little useful detail, although a transverse lineation is well preserved.

HOLOTYPE. I.8640 (B). Fig. 69.

DIMENSIONS. Length of mesothorax 3.0 mm, of tegula 1.5 mm.

REMARKS. The general habitus, M absent from the discal cell, M_2 close to M_3 basally in both wings and hindwing with $Sc+R_1$ close to Rs beyond the discal cell are indicative of the Pyraloidea : Pyralidae (Common 1970 : 833, 836). The venation approaches the Recent genera *Paractenia* Ragonot, *Bostra* Walker, *Diloxia* Hampson and *Tyndis* Ragonot (cf. Hampson 1896 : figs 101, 104, 105, 111) in the Pyralinae (and Pyralini of Whalley 1961). The fossil agrees with *Pyralites obscurus* Heer from Aix, southern France (mid-Oligocene, Denizot 1956 : 5) in having a rounded mesothorax, but differs from the latter in the larger size of the mesothorax and in having a distinct mesothoracic scutoscuteellar suture (cf. Heer 1856 : 30; pl. 2, fig. 6). However, a re-examination of *P. obscurus* may require a separate genus for *P. preecei* sp. nov.

The adults of Recent pyralids are usually nocturnal insects, pyraline larvae generally feeding on dry or decomposing vegetable material (Bourgogne 1951 : 399-400). The subfamily has a widespread distribution.

Superfamily GEOMETROIDEA

Family GEOMETRIDAE

Genus *GEOMETRIDITES* Clark *et al.*, 1971

TYPE SPECIES. *Geometridites repens* Kernbach 1967, by original designation of Clark *et al.* 1971; Pliocene, Willershausen.

Geometridites larentiiformis sp. nov.

Fig. 71

DIAGNOSIS. A fossil species of Geometridae with the forewing venation resembling that of the extant larentiine *Chloroclysta truncata* (Hufnagel), but differing in that R_{2-5} are not curved apically.

DESCRIPTION. Fragment of a forewing, estimated original length 15 mm. Sc represented by a short median portion. Two elongate areoles present, the inner smaller than the outer; R_{2-5} from apical extremity of latter, the separation of R_1 a little more basad. R_{2-4} with common stem, base of R_2 equidistant between that of R_3 and areole. M_1 gently curved and continuous with stem of R . CuA_2 and $1A+2A$ represented by two short sections, strongly divergent and indicating a broad wing.

HOLOTYPE. I.8866 (B) and counterpart I.8935 (B). Fig. 71.

DIMENSIONS. Length of inner areole 1.5 mm, of outer areole 2.1 mm; fork of R_{3+4} 2.4 mm from latter.

REMARKS. Sc separate from R , two areoles anterior to the apical end of the discal cell, R_5 with areolar origin, and general form of the venation place the wing in the Geometridae in the Sterrhinae or Larentiinae (Common 1970 : 846, 848). The venation is especially close to some Recent Larentiinae (cf. Fig. 70) but the fossil is too incomplete for certain subfamily placing; its clear geometrid affinities render it referable to the broad fossil genus *Geometridites* Clark *et al.*

Both Recent subfamilies have a cosmopolitan distribution, the Larentiinae with a temperate preference (Bourgogne 1951). Geometer larvae are found on foliage, usually pupating in the ground or amongst débris (Common 1970 : 846).

Superfamily PAPHILIONOIDEA
Family NYMPHALIDAE

Genus *NYMPHALITES* Scudder, 1889

TYPE SPECIES. *Nymphalites obscurum* Scudder 1889, by original designation; Oligocene, Florissant.

Nymphalites zeuneri sp. nov.
Figs 72, 75-6

- 1878 *Lithosia* (sp.); Smith in Woodward : 88.
1879 *Lithosia* (sp.); Smith in Woodward : 344.
1894a Butterfly; Scudder in Brodie : 168.
1894b Butterfly; Scudder in Brodie : 70.
1907 (? *Lithosia*); Handlirsch : 923.
1961 cf. *Euthalia*; Zeuner : 310.

DIAGNOSIS. Medium-sized Palaeogene species of Nymphalidae close to the Recent species *Neurosigma siva* Westwood, *Abrota mirus* Fabricius and *Cymothoe theobene* Doubleday & Hewitson in wing form and venation, but the forewing differs in that M_2 is less close to M_1 basally and the hindwing is differentiated by the short humeral vein towards the humeral angle and relatively narrow anterior area of the wing.

DESCRIPTION. The body is represented by some black chitinous fragments of the thorax near the cleaved edge of the rock, the remainder apparently having broken away during collection.

The remains of both pairs of wings are preserved on the opposite sides of I.10384. The two pairs diverge from the body at an angle of about 15° resembling the upright rest position of the wings in butterflies. However, the hindwings are here overlapped on the outside by the forewings, indicating that they are folded beneath the body as may happen in dead Recent specimens. The two wings on either side are separated from each other at many points by a fine parting of limestone, although this has flaked away in places on I.10384a exposing the forewing. The following account is based on the left pair (Figs 72, 76) as only the bases of the right pair are exposed and these are similar to the left.

Forewing: moderately wide, outer part missing. Discal cell closed, elongate and widest near origin of R_1 with maximum length to width ratio 3.4 : 1. Cells C and Sc moderately narrow. R_1 arising 0.7 of the length of the discal cell from base. R_2 closer to R_{3-5} than R_1 but well separated from the former. R_{3-5} and M_1 arising from the anterior apical angle of the discal cell; stem of R_{3-5} 0.4 of the cell length and only the initial portion of the first fork preserved. Cu trifold, CuA_1 and CuA_2 with relatively divergent courses and separating at 0.8 and 0.5 respectively of the length of the discal cell from base. M_2 closer to M_1 than M_3 at 0.4 of the span between the bases of M_1 and M_3 . Branches of M gently curved towards outer margin. Discocellular crossvein fine but clear : udc absent, mdc curved basally and ldc nearly straight. 1A + 2A single.

Hindwing: moderately elongate, margins missing except for the basal part of the anterior margin. Discal cell apparently open and broader than in forewing: about 0.66 of the length of the forewing cell. Cell Sc + R_1 wide. Humeral area expanded, angular. Humeral vein indicated by a straight groove just over 1 mm long arising from the fork of Sc + R and directed towards the humeral angle. Rs slightly sinuous. M_2 closer to M_1 than M_3 . Cu trifold, CuA_1 and CuA_2 divergent arising in the outer half of the discal cell. Inwards of 1A + 2A on I.10384a are some traces of wing membrane which apparently include fragments of the anal area, but these are difficult to separate from the right wing pair which is very close at this point. The hindwing shows faint impressed traces of the forewing venation.

Colouration: both wings show a light brown pigmentation which is better preserved in the hindwing. The ventral counterpart of the hindwing shows the underside colour pattern (Fig. 72a). This includes two dark brown lines in the outer part of the discal cell, another traversing cells C and Sc + R_1 and an irregular postdiscal band. The last consists of broad crescents with dark

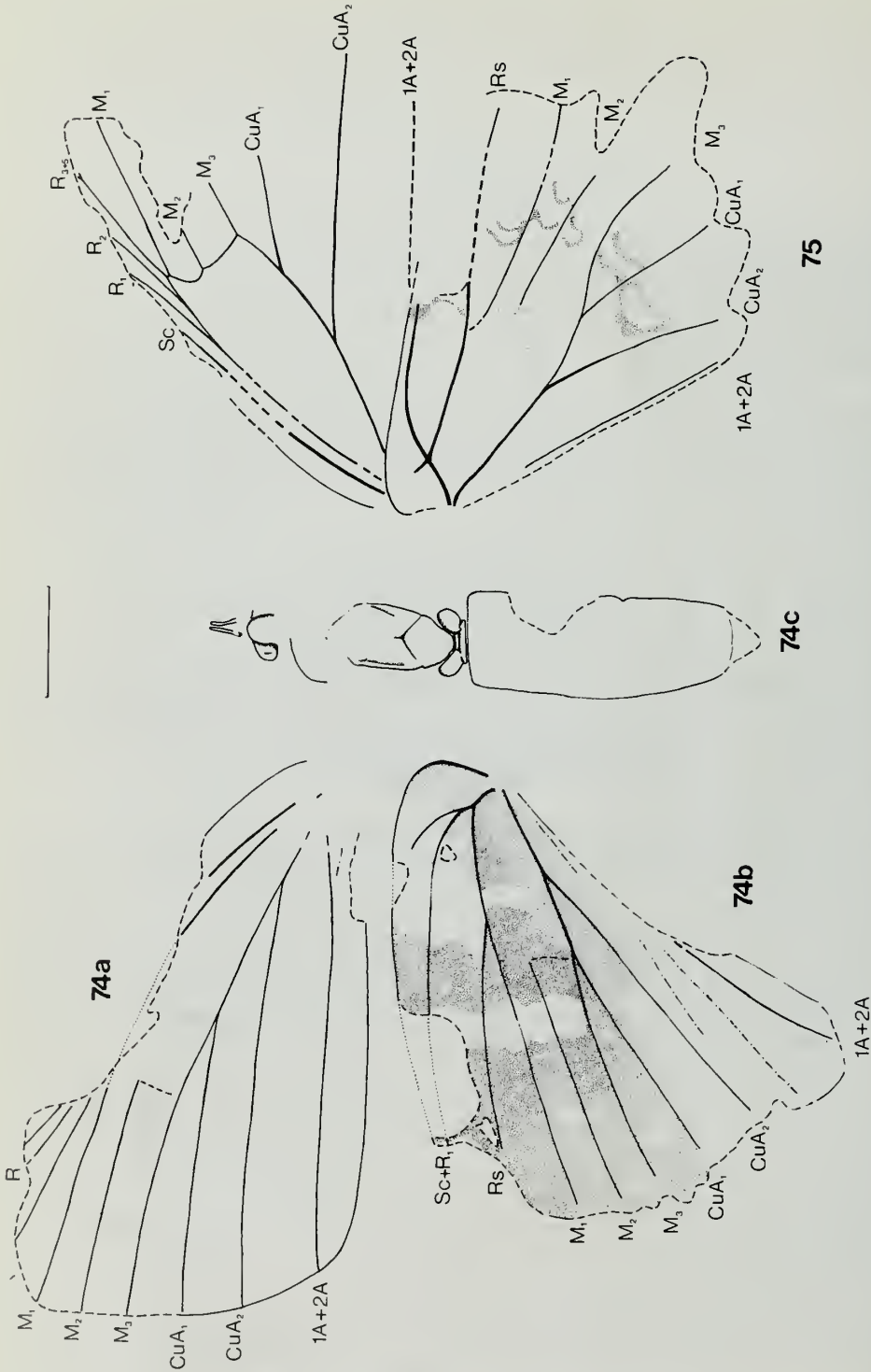


Fig. 74 *Lithopsyche antiqua* Butler. Holotype. Fig. 74a, left forewing based on details from part and counterpart. Fig. 74b, left hindwing after removal of forewing on counterpart (I.10369) with some details from part (I.19984). Fig. 74c, body : head and abdomen from counterpart, thorax in dorsal aspect from part. See also Fig. 77.
 Fig. 75 Wings of *Nymphalites zeuneri* sp. nov. Holotype in ventral aspect, orientation conventional. I.10384. See also Figs. 72a, b, 76. (Scale line = 5 mm)



Fig. 76 *Nymphalites zeuneri* sp. nov. Holotype (part). I.10384. See also Figs 72a, b, 75.
Fig. 77 *Lithopsyche antiqua* Butler. Holotype (part). I.19984. See also Figs. 74a, b, c.
(Scale line = 5 mm)

brown margins and pale centres; it is interrupted in cell M_2 and offset basally in cell Rs. The discal line in cells C and Sc + R_1 shows traces of a pale area near Sc on its outer side.

HOLOTYPE. I.10384 (B) and counterpart I.10384a (B). Figs 72a, b, 75, 76.

DIMENSIONS. *Forewing*: maximum width of discal cell (opposite the base of R_1) 4.0 mm, length 13.5 mm.

Hindwing: base of M_1 to base of CuA_2 , 4.4 mm; base of discal cell to base of M_2 , 9.2 mm.

REMARKS. The general habitus of the fossil is indicative of the Nymphalidae. Zeuner (1961) regarded it as close to the Recent genus *Euthalia* Hübner, but his proposed description (*ibid.*) was never published. However, a note in the fossil insect collection at the BM(NH) indicates that he regarded it as nearest to the allied *Tanaecia pelea* Fabricius (= *T. pulasara* Moore). This species differs principally from the fossil in that the forewing lacks crossvein ldc and the hindwing has an apically curved humeral vein which originates from Sc + R_1 distad of the fork of Sc + R (Schatz & Röber 1885-92 : pl. 26). The absence of ldc in the forewing is also characteristic of *Euthalia* Hübner (Bingham 1905 : 267), the venation of which is very similar to *Tanaecia* Butler (Schatz & Röber 1885-92 : pl. 26). It is possible that Zeuner's comparison with *T. pelea* was based on the large crescentic markings of the postdiscal band in the hindwing of this Malayan species, but the band is more irregular and of a different form in the fossil.

Zeuner (1961 : 310) stated that this is the fossil which Handlirsch recorded as *Lithosia* Fabricius, a living genus of arctiid moth, based on an old label. Handlirsch (1907 : 923), however, queries the identification of *Lithosia* in the Insect Bed and gives Woodward (1879) as the source of the record. Radcliffe-Grote (1901) also doubted the identification. The determinations in Woodward's paper (by F. Smith) were based on material received from A'Court Smith, and although the specimen is from Brodie's collection it is quite likely that it subsequently went to the latter, for Brodie (1878) mentions that he obtained material from A'Court Smith. Specimen I.10384a is actually labelled *Lithosia* in Brodie's hand, but on labels in the same hand accompanying I.10384 the latter is recognized as a butterfly hindwing accompanied by Scudder's name. Brodie (1894a, b) published the determination made by the latter.

The venation of the fossil does not resemble *Lithosia*, but comes close to that of the living nymphalid species *Neurosigma siva* Westwood, *Abrota mirus* Fabricius and *Cymothoe theobene* Doubleday & Hewitson (Schatz & Röber 1885-92 : pls 24-26). It differs principally in that in these Recent species the forewing appears to have an incipient second anal and M_2 is much closer to M_1 basally; the hindwing has a longer humeral vein which is curved apically and the anterior part of the wing is wider. The venation of the fossil also resembles that of the living *Aeropetes* [= *Meneris*] *tulbaghia* (Linné), but the forewing of the latter differs in that R_2 is closer to R_1 , mdc is not curved basally, and in the hindwing the humeral vein has a slight basal curve, M_2 is more central between M_1 and M_3 , and ldc is present (Schatz & Röber 1885-92 : pl. 35).

The colour pattern of the fossil does not agree with specimens of the above Recent genera in the collection of the BM(NH) nor with any of the butterflies illustrated in Seitz (1909-39). Of the known Palaeogene genera of Nymphalidae the fossil can only be placed as a separate species in the broadly-based genus *Nymphalites* Scudder.

Personal observations on the decay of the wings of *Inachis io* (Linné) in water indicate that the darker browns remain when the brighter colours have faded. Considering that the wings of other insects in the Insect Bed may preserve a dark brown colouration essentially similar to Recent relatives, e.g. the hemerobiids described herein, it seems likely that the dark brown markings in *Nymphalites zeuneri* are original, with a light centre in the postdiscal band.

Recent Nymphalidae are a large, cosmopolitan family feeding on a variety of angiosperms.

Family LYCAENIDAE

Genus *LITHOPSYCHE* Butler, 1889

(non *Lithopsyche* Scudder, 1889, = *Lithodryas* Cockerell, 1909)

1974 *Calospilites* van Schepdael : 15, 18.

TYPE SPECIES. *Lithopsyche antiqua* Butler 1889 : 294; pl. 21, fig. 3; by monotypy.

Lithopsyche antiqua Butler 1889

Figs 74, 77

DESCRIPTION. *Body*: the head is preserved as a rough cast on the counterpart and shows few details; labial palpi elongate. An external mould of the dorsal surface of the thorax is well preserved in the part; mesothorax elongate, scutoscutellar suture distinct, arcuate; metathorax short, expanded laterally. Abdomen dorsoventrally compressed with scale traces especially at the posterior end.

The following account of the wings is based on the left pair which are well separated from each other by matrix. The right pair are superimposed and their anterior parts are missing; what can be discerned of the venation is similar to the left pair.

Forewing: original span estimated at 60 mm. Costal area moderately wide, Sc represented only by basal portion. Three divergent branches of R are preserved apically. Discal cell elongate, about 0.2 as wide as long. M_{1-3} nearly parallel, with a median M_2 and faint trace of Idc. $1A+2A$ with traces of a basal fork.

Hindwing: broad, cells C and Sc + R_1 expanded. Humeral angle rounded with margin thickened on its inner side. Humeral vein curved apically, originating very close to the separation of Sc + R_1 . Discal cell short, 0.55 of length of forewing cell. M similar to forewing, CuA_1 separating near the posterior end of Idc. $1A+2A$ represented by a distal portion and well separated from CuA_2 . Anal area largely obscured by the abdomen.

HOLOTYPE. I.19984 (S) and counterpart I.10369 (B). Figs 74a, b, c, 77.

DIMENSIONS. Length of discal cell 15 mm (forewing) and 8.2 mm (hindwing).

REMARKS. Scudder (1883 : 280) used the generic name *Lithopsyche* for a Palaeogene nymphalid from Florissant, but this was a *nomen nudum* and a full description was not published and a type species designated until 1889. In the same year Butler independently described the present genus of geometrid moth from the Insect Bed using the same name, and thus created a homonym. Butler's paper is dated 21st May but was not published until October (Duncan 1937). Scudder's paper has no month of publication although the advertisement with which it is bound is dated 1st October. The original wrapper of the part in which Butler's paper appeared is preserved in the Zoology Library, BM(NH), bound with the journal; the date of issue is given as 1st October. Butler's name therefore would seem to have priority and the replacement name inadvertently offered by van Schepdael to be superfluous and invalid.

Butler saw only the part (I.19984), of which he published a colour lithograph (1889 : pl. 21, fig. 3). Under normal lighting neither half (Fig. 77) shows evidence of the colour banding in Butler's figure, although browns are well preserved in other Insect Bed Insecta. Examination under ultraviolet and infrared lighting only emphasizes some vague traces of pigmentation in the forewing (Fig. 74a). The left hindwing, now exposed on the counterpart, shows some well-preserved brown mottles (Fig. 74b).

Butler compared the fossil with 13 species of extant Geometridae, and specimens of these have been examined. Their only resemblance is that they show much dark pigment in their wing colouration: the venation is quite different. The wing form and venation of *Lithopsyche* Butler is, however, close to that of the extant Riodininae species *Metacharis ptolomaeus* (Fabricius), *Mesene phareus* (Cramer), *Anteros formosus* (Cramer), *Theope publius* Felder, *Uraneis hyalina* (Bates) and *Polystichtis emylius* (Cramer) (Schatz & Röber 1885-92 : pls 43-45; Stichel 1910-11 : pls 8, 13, 15, 22). It differs principally in that there is no evidence of a fork in the outermost branch of R; however, the latter is incomplete in the fossil and a terminal fork may have been developed. The fork is absent in some extant Lycaeninae, e.g. *Neolycaena* de Nicéville.

Recent Lycaenidae are a large, cosmopolitan family feeding on a variety of angiosperms; the larvae are frequently myrmecophilous.

? Superfamily PAPILIONOIDEA

Genus *indet.*

Fig. 73

DESCRIPTION. The single specimen consists of a decapitated body with wing remains. The thorax is uncrushed but few details are discernible due to mineralization. Abdomen elongate, flattened dorsoventrally except near base and apex; the lateral interior of the basal segment contains traces of cream-coloured calcified muscle, and the apical segments are covered with a dense coat of piliform scales.

Forewing: (In.64545a, left, Fig. 73). Cells C and Sc moderately narrow. Discal cell elongate, slightly constricted apically and apparently open. Sc terminating on the costal margin a little distad of the end of the discal cell. Branches of M only slightly divergent and gently inclined relative to the long axis of the cell; M_2 nearly equidistant between M_1 and M_3 . R_1 originating at 0.7 of the length of the discal cell from base, R_2 and R_{3+4} originating close together where the cell begins to constrict; R_4 parallel to M_1 . CuA_1 leaves the cell opposite the base of R_2 and CuA_2 a little basad of base R_1 . The posterior part of the forewing is obscured by the corresponding hindwing.

Little further can be said concerning the venation except that the veins immediately to the right of the abdomen (In.64545a) are probably CuA and an anterior anal of the opposite hindwing. There is no indication of colour pattern on the wings although scale traces may be discerned at higher magnification.

MATERIAL. In.64545a, b (H). Fig. 73.

DIMENSIONS. Abdomen: length 13 mm. Forewing: estimated original length 20–25 mm; length of R_{3+4} stem. 3.4 mm.

REMARKS. The size and venation place the fossil amongst the higher ditrysian macrolepidoptera. The forewing venation bears a general resemblance to some Lycaenidae (cf. Bingham 1907: figs 72–73), including *Curetis siva* Evans and *Ogyris genoveva* Hewitson, although there are differences in detail. The close proximity of the two outer branches of R resembles certain Nymphalidae, e.g. *Apatura iris* (Linné), although the venation differs in other respects such as in the position of M_2 . The fossil probably belongs to the Papilionoidea, though in the absence of further material the placing is uncertain.

The abdominal muscles probably underwent mineral replacement like some seeds from the Insect Bed, where the endospermal cells are replaced by a 'cream-coloured granular substance' (Reid & Chandler 1926: 7).

Conclusions

During late Eocene and early Oligocene times southern Hampshire and the northern part of the Isle of Wight are considered to have formed part of a wet coastal lowland subject to marine inundation; gradual crustal subsidence resulted in the accumulation of tens of metres of sediment. The Bembridge Marls represent one such marine transgression with a much longer regressive period (Daley 1973a). Unique conditions near the base of this deposit resulted in the formation of fine-grained limestone in a unit sandwiched between brackish-water clays (*ibid.*), thus preserving the fragile water-logged remains of various small and medium-sized Insecta; the associated biota has already been discussed (p. 239). Insect orders represented are Hymenoptera, Diptera, Coleoptera, Neuroptera, Mecoptera, Lepidoptera, Trichoptera, Hemiptera, Thysanoptera, Psocoptera, Isoptera, Dictyoptera, Orthoptera, Plecoptera, Odonata and possibly Dermaptera. Of these the first three constitute over 70% of the insects in the collections examined, the first two being especially common: more than 120 species of Diptera and Hymenoptera have been described. Although taxonomically diverse, the insects considered in the present paper represent about 1.5% of the total number of insects in the collections examined. The A'Court Smith

collection, much of which went to Brodie and to Hooley (p. 239), is biased towards better-preserved material, for Brodie states 'Mr Smith observes that owing to the perverse fracture he has lost a very considerable number of specimens . . .' (Brodie 1878 : 9) The A'Court Smith, Hooley and Brodie collections at the British Museum (Natural History) contain some 9000 insects. A bulk sample collected in 1975 yielded nearly 700 insect remains. Of the orders studied, the numbers of specimens in the main collections compared with the sample (the latter in parenthesis) are: Isoptera 92 (2), Plecoptera 1 (0), Neuroptera 10 (1), Mecoptera 2 (0), Lepidoptera 24 (1). The proportional representation of these orders is therefore broadly similar except in the Isoptera and here the most common species, *Mastotermes anglicus* von Rosen, is a relatively large insect and collector's bias is to be expected.

The Lepidoptera proved the most taxonomically diverse in this study, with 24 species ranging from pollen feeders to non-feeders amongst the adults and both surface feeders and miners amongst the larvae. The Bembridge fauna includes the most primitive Lepidoptera (Micropterigidae) through to the most advanced (butterflies); adult *Micropterix* occurs with its food plants (*Ranunculus*, *Carex*) in the same bed. Of the orders considered here the Lepidoptera are the most diverse in the British and world fauna at the present day with a total of over 165 000 known species. They are usually thought to be very rare as fossils but that is probably partly because the small species are overlooked; however, these specialized terrestrial insects cannot be expected to form a significant part of an aquatic death assemblage. Further work on some of the microlepidoptera from the Insect Bed, such as scanning electron microscope examination for aculae, may help to clarify their affinities. The Neuroptera (Sisyridae excepted) and Mecoptera are represented by families in which both adult and immature stages are terrestrial and, like the Lepidoptera, their infrequency in an aquatic sediment is not surprising. The bionomics of Recent hemerobiids and chrysopids (Neuroptera) are very similar and both are active predators of plant-feeding insects such as aphids and coccids (Balduf 1939 : 250, 292). Aphids are present in the Insect Bed and since the chrysopids and hemerobiids are close to extant forms, it is quite likely that they had a similar ecological role in Bembridge Marls time. The Mecoptera are represented in the Insect Bed only by Bittacidae and there is no evidence of Panorpidae or Boreidae in British Palaeogene strata, the only two families of Mecoptera in Britain at the present day. Carpenter (1954), from a study of Baltic amber, concluded that bittacids were more diverse during the Palaeogene than today, although the virtual absence of resin in the British Tertiaries and its abundance in contemporaneous strata in the Baltic area (Larsson 1978) is somewhat puzzling.

Aquatic insects in the orders studied are represented by the Neuroptera (Sisyridae) and Plecoptera, but these freshwater groups are only known from two incomplete wings of the terrestrial imagines which suggests a limited development of local freshwater habitats; my observations on the Insect Bed Trichoptera tend to support this as the order is relatively rare and taxonomically restricted.

The occurrence of four families of termites indicates a warmer climate than today in the Hampshire Basin during Bembridge Marls time. At the present day their normal poleward limit in the Palaearctic is latitude 45° N (Harris 1970 : 295). Kalotermitids, rhinotermitids and termitids overlap south of about latitude 35° N in the eastern Palaearctic (*ibid.*). In the southern hemisphere the poleward limit of *Mastotermes* is at the Tropic of Capricorn: the northern tropic approximates to the equatorial limit of *Reticulitermes*. The evidence from the termites therefore suggests that, in temperature terms, the palaeoclimate was close to the warm temperate (sub-tropical)–tropical boundary in the sense of Miller 1961. This is compatible with the evidence from the other groups studied. Daley (1972*b*) has suggested that the Eocene climate of Britain was such as to allow some overlap of modern tropical and temperate biotas and this would facilitate the coexistence of *Reticulitermes* and *Mastotermes*. The Insect Bed Isoptera are represented by alates which only emerge in the open for their ephemeral swarming-flights. The bodies are preserved in many specimens of *M. anglicus*, often with visible appendages, suggesting a fairly local provenance. The occurrence of *Ficus* in the Insect Bed is of ecological interest as this is one of the woody plants which is resistant to attack by extant *Mastotermes*; the occurrence of this termite also suggests that precipitation was less than that of modern rainforest. The Insect Bed termites are represented by wood-feeding forms with one possible exception (p. 253). Modern

Termitidae include many non-lignivorous species and the single detached wing suggests derivation from a more distant habitat, perhaps in more open country.

The British insect fauna in Bembridge Marls time included a number of groups not represented here at the present day. In addition to the Isoptera, other notable absentees include the Bittacidae, Mantispidae and Copromorphidae; the distribution of these and the other taxa is discussed above.

The Insecta are a very diverse group at the present day and were undoubtedly already so in more recent geological times. Many of the characters used by modern entomologists for generic and specific classification are often missing or poorly preserved in fossils. Whilst this does not preclude the possibility of a satisfactory fossil taxonomy, the task of relating Tertiary fossils precisely to their extant relatives is difficult: further collecting and comparative study will probably help to clarify relationships. Meanwhile the fossils provide useful data on Tertiary distribution, ecology and comparative morphology of many modern groups.

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